AN ECOLOGICAL STUDY OF THE MACRO-INVERTEBRATE FAUNA OF THE EERSTE RIVER WESTERN CAPE PROVINCE, SOUTH AFRICA

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Thesis presented for the degree of PhD.

ZOOLOGY DEPARTMENT

University of Cape Town

November 1982

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INTRODUCTION

South Africa is a country of varied rainfall, from the summer rains of the Transvaal to the winter rains of the south-western Cape, and from the non-seasonal and relatively high amounts that fall in the eastern Cape to the very sparse and unpredictable rainfall of the western and central regions. As most areas receive either an intermittent or seasonal rainfall, drought is a constant threat in this fast-developing country and, with a rapidly increasing population to cater for, the provision of ever greater amounts of water is a matter of vital importance. To date most of this water is provided by the country's rivers, there being little accent on alternative sources such as recycled waste-water or de-salinated sea water. Almost all major rivers are now regulated by dams, and it has been predicted that by the next century very little fresh water will reach the sea. Quite simply, we are losing our rivers before we have had the chance to study them as ecological units.

The first detailed biological and chemical study of a South African river was that of the Berg River in the western Cape, which was undertaken by A.D. Harrison and J.F. Elsworth in 1950. Over the next two decades hydrobiological studies on other major rivers within the Republic were completed by B.R. Allanson, F.M. Chutter, A.D. Harrison, W.D. Oliff and others, and these provided a good knowledge of the countrywide distribution of riverine species and the adjustments of the

biota to changing climates across the country. These authors also dealt with the relation of the distribution of the animals within rivers to the physico-chemical quality of the water, thereby forming the basis of our present knowledge of the biotic changes associated with pollution of river water.

Since these studies biological work on the country's rivers has come to a virtual halt and, to date, such basic data as the invertebrate standing stock, in any river in South Africa, have not been published. No modern ecological studies of river catchments have been carried out, and information such as life cycles, and the feeding and reproductive biology of riverine species, is confined to those of medical or commercial importance. We need a better understanding of the ecology of our rivers and of the biology of the riverine biota, in order to be able to predict the biological adjustments that will accompany environmental change. Without this knowledge river biologists are in a poor position to aid those in authority in drawing up sensible management programmes for river systems.

From a scientific point of view, the south-western Cape Province of South Africa is an exceptionally interesting area. Unlike the rest of the country the region has a temperate climate, a typical Mediterranean winter-rainfall pattern and supports an endemic heath-like vegetation known as fynbos, which is extremely rich in species. The high degree of endemism displayed by fynbos species is reflected in the rivers that run through the fynbos biome, for many of their invertebrate species are found only in headwaters of the region. These

rivers are under the same pressures as rivers throughout the country, with dams constructed on their headwaters and a variety of pollutants entering their lower reaches. Additionally, the creation of impoundments in the mountain catchments is reducing the total area of mountain fynbos, while manipulation of the vegetation there, to produce the maximum run-off of high-quality drinking water, may be threatening its integrity in ways we do not comprehend yet.

One river running through the fynbos biome, the Eerste River, was chosen for this study with the aim of acquiring some understanding of the ecology of a representative stream of the region. The Eerste (or First) River was the first river that early settlers came upon after leaving the settlement at the foot of Table Mountain and travelling across the inhospitable and sandy wastes of the Cape Flats. It is a perennial stream rising in one of the most southerly mountain ranges in Africa, and displays the typical flow pattern of rivers of the south-western Cape - discharge is very low during the dry summer months, but is high in winter with occasional very powerful spates. The river runs through undisturbed mountain fynbos in its upper reaches and then through agricultural areas to its estuary.

The thesis is presented as a series of four papers, of which the first has been published and the second is presently in press, and concludes with a summary. The four parts deal with discrete topics, yet are closely related, each building on the knowledge supplied by the earlier parts. Following the summary is a supporting paper of a more generalised nature, which provides background information on the

limnology of the south-western Cape. As the papers had to comply with the different requirements of the scientific journals to which they were submitted, some journalistic differences exist between the parts; the most obvious of these is the use of either a decimal point or a comma to separate unit figures from fractions of a unit.

At the beginning of the study, the temporal and spatial changes in species and standing stock of the invertebrate fauna of the river were recorded, and these changes were related to the changing physico-chemical quality of the water (Parts 1 & 2). This provided a basic picture of the river's ecology. The biomass figures given in Part 2 are the first documented in this country for the standing stock of riverine invertebrates.

Data on the Ephemeroptera in the system were then synthesised (Part 3), as these animals are numerically important in rivers throughout the country. They lend themselves to investigation, as they are relatively easy to identify to the level of species, unlike the other numerically-dominant and ecologically-important group, the Chironomidae. The Ephemeroptera are known to be sensitive to environmental changes and this, together with their widespread abundance, makes them potentially useful tools for monitoring the health of our rivers. The data on Ephemeroptera presented in this thesis are the first dealing with the life cycles, growth rates and voltinism of the group in this country.

Investigations of the secondary production of the mountain stream

section of the Eerste River, which runs through mountain fynbos, were then undertaken (Part 4). These investigations were stimulated by the current interest in, and concern for, the future of fynbos, which centres around the Fynbos Biome Project within the National Programme for Environmental Sciences, which is administered by the Council for Scientific and Industrial Research. Fynbos constitutes one of the six botanical Kingdoms of the world, and is a vegetation of great beauty, ranging from the succulent and sclerophyllous leaf-forms of coastal strandveld to the evergreen shrubs and trees of mountain fynbos. Though the mountain streams running through fynbos are generally recognised as having a low secondary productivity, and though leaf-litter from fynbos must be profoundly implicated in the low productivity of these shaded and nutrient-poor headwaters, the relationship between the two has never been investigated. In Part 4 I describe and give the results of a series of investigations into the dynamics of allochthonous detritus in the Eerste River, and into the growth of a riverine detritivore when fed leaf species that were common in the detritus. These investigations are a first attempt to identify the causes of the low secondary productivity of headwaters of rivers that run through the fynbos biome.

ACKNOWLEDGEMENTS

Many people were generous with their time and help, and I have acknowledged them gratefully in the appropriate parts of the thesis. I would like to mention here the people who have contributed in a more generalised way, or over a long period of time, toward the completion of this thesis. My husband Jim unfailingly supported me in my work, and footed the bill for many of the expenses involved in the field trips and experimental work. My supervisor, Professor George Branch, patiently and expertly guided my thinking and writing along more scientific lines, and encouraged me to continue when it seemed impossible to do so. To these two people I extend my heartfelt thanks.

Denise Green (nee Gibbons) and Anne Stewart (nee Moore) assisted on the field trips and in the tedious tasks of sorting samples and recording the data. Their cheerful companionship, and willingness to turn out in all weather conditions or to do any kind of job, contributed enormously to the success of the work. Finally, my thanks to Leonora Fox, who typed most of the thesis and advised me on several problems concerning its publication.

The work was partially financed by the Percy FitzPatrick Institute of African Ornithology, the University of Cape Town and the Council for Scientific and Industrial Research.

PART 1

THE DISTRIBUTION OF INVERTEBRATE COMMUNITIES IN A SMALL SOUTH AFRICAN RIVER

Hydrobiologia 83, 43-65 (1981)

The distribution of invertebrate communities in a small South African river

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Keywords: river, aquatic macroinvertebrates, lotic environment, seasonal changes, longitudinal zonation, cluster analysis, multiple discriminant analysis.

Abstract

Monthly samples of macroinvertebrates were collected from the stony-bed and marginal-vegetation habitats of a small river in the south western Cape Province, South Africa. Cluster analyses of the samples revealed assemblages of invertebrates (here referred to as 'communities') with clear spatial and temporal distribution patterns in the river. The species composition of the communities, and their distribution, are described. The relation of the macroinvertebrate distribution to changes in the physico-chemical environment was investigated using stepwise multiple discriminant analysis. The results indicated a strong correlation between the two.

Introduction

Past investigations into the hydrobiology of South African rivers have centred on a few of the longer or more prominent river systems, in particular the Berg (Harrison 1958a, 1958b; Harrison & Elsworth 1958), the Jukskei-Crocodile (Allanson 1961), the Tugela (Oliff 1960a, 1960b, 1963; Oliff & King 1964; Oliff *et al.* 1965) and the Vaal (Chutter 1963, 1970, 1971; Harrison *et al.* 1963). These early surveys produced a reasonable understanding of the factors influencing the distribution and abundance of riverine fauna, but subsequent hydrobiological work on the country's rivers has been sparse.

The southern and eastern coasts of South Africa have an abundance of short rivers, none of which have been studied in detail. They rise in coastal hills and drop steeply to narrow coastal plains, and thence to the sea. Most of them have the same longitudinal sequence of physical zones as neighbouring, longer rivers (Noble & Hemens 1978), and are subject to some combination of the same interferences and pollutants (e.g. water extraction, fluvial sediment, organic effluents and agricultural runoff). Their simple profiles and short zones make them particularly suitable systems for studying changes in the biota along a river, and for tracing the factors that cause these changes.

The Eerste River is a short (40 km) river in the south western Cape Province (Fig. 1). The present limnological investigations of its stony-bed section – the upper 26 km – began in March 1975. In this paper, the spatial and temporal changes in species composition of macroinvertebrates of the two major habitats – the stony-bed and marginal vegetation – are described. Distribution of the animals in the river is shown to be related to differences in the physical and chemical character of the river.

The study area

South Africa is subject to seasonal rains, which fall in summer (December to February) over all but the southern and south-western tip of the country. This latter, boomerang-shaped strip of land has a mediterranean climate with a typical

Hydrobiologia 83, 43–65 (1981). 0018-8158/81/0831-0043/$04.60.

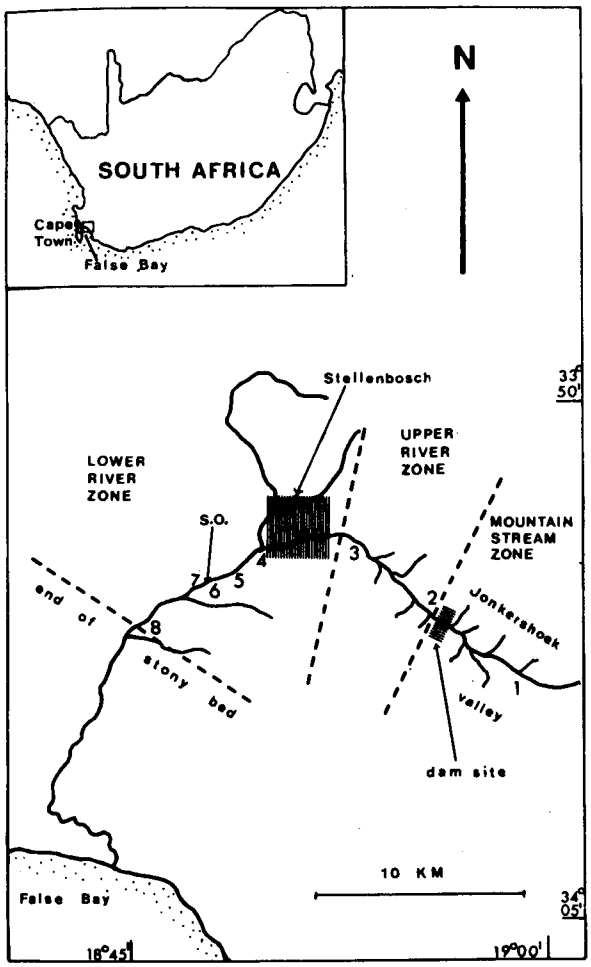

Fig. 1. The Eerste River, showing the eight sampling stations (1–8), the dam, and the sewage outfall (S.O.). The three physical/biotic zones identified in the survey are shown.

winter (June to August) rainfall pattern. Further climatic information is given in Schulze (1965).

The Eerste River lies in the winter rainfall area. It rises in the Dwarsberg Mountains, 60 km east of Cape Town (Fig. 1). Yearly rainfall over its catchment ranges from 3 000 mm on the mountains to 700 mm or less on the coastal plain (Van der Zel 1971), with about 80% of the rain falling in a series of winter downpours, which bring the river down in spate. Only 7% of the annual precipitation occurs between December and March, and as water is continually extracted from the river for urban and rural use, flow may cease in its lower reaches during these months. The upper 26 km of the river, which was the study area, consists of runs, riffles and occasional deep pools, with water less than 1 m deep except during spates. Within the study area there are three distinct physical zones (Fig. 1).

The Mountain Stream is a 7 km stretch from the source to the lower end of the Jonkershoek valley. The stream is 5–7 m wide, with an average gradient of 24 $m.km^{-1}$. The substrate consists of boulders, large stones and bedrock. Algal growth is sparse and marginal vegetation is confined to occasional clumps of palmiet *Prionium serratum*. The surrounding mountain slopes form part of a Forestry Reserve; they support fynbos, the indigenous, sclerophyllous flora of the southern and south western Cape, and plantations of *Pinus radiata*. Several species of tough-leaved, evergreen trees (e.g. *Metrosideros angustifolia, Brabejum stellatifolium*), most of which are confined to the fynbos biome, line the river. A dam is presently under construction at the lower end of the valley.

The Upper River is a 5 km stretch through foothills covered with vineyards. The average gradient is 12 m/km and the width 7–11 m. Substrate and marginal vegetation are similar to those in the Mountain Stream, and algal growth is sparse except for some *Spirogyra* in summer. The exotic oak *Quercus robur* replaces indigenous trees along the banks.

The Lower River is a 14 km stretch onto the coastal plain, through agricultural land and orchards. The substrate consists of stones and pebbles on coarse sand. The river's width increases to 8–18 m and the average gradient drops to 2 $m.km^{-1}$. Mixed evergreen and deciduous trees line the banks, with *Q. robur* and another deciduous exotic, *Populus canescens* numerically dominant. Marginal vegetation is abundant and sewage fungus (see Hynes, 1960) covers the rocky substrate in the dry season. Stellenbosch, the only town on the river, is at the junction of the Upper and Lower Rivers. The town has no heavy industry, but winery and sewage effluents enter the Lower River, mostly via a sewage farm situated 3 km below the town.

Methods

Stations

Samples were collected at monthly intervals between March 1975 and April 1976, from eight

stations (1–8) along the river (Fig. 1); Table 1 gives details of the locations. Station 5 was abandoned in October 1975, because of its similarity to stations 4 and 6, while station 8 was created in September 1975, though some samples were collected there earlier.

Physical and chemical variables

Measurements of dissolved oxygen (YSI Oxygen Meter), pH (Beckman Portable pH Meter), water temperature and current speed (Rigosha Small Flow Meter) were taken in the field. Water from the mountain stream was not analysed, but Steer (1966) reported that it was of high quality and free of pollution. Monthly water samples from stations 3, 4, 6, 7 and 8 were tested for nitrite and nitrate using a Technicon autoanalyser; total phosphate-phosphorus, by the Colorimetric Molybdate-Vanadate Technique (Martin & Marais 1975); and total alkalinity using the standard method described by the Am. Pub. Health Ass. (1971). The physical and chemical data were arranged into a number of 'water samples', each corresponding to a faunal sample in time and place of collection, and containing one value for each of the variables.

Sampling the fauna

Stony-bed animals were collected using a square-framed sampler, that sampled 0.25 m^2 of river bed. The upstream and two adjacent sides were covered with sheeting through which water could flow, while the downstream side held a net with mesh size 0.6 mm. When the sampler was placed on the river bed, a fringe of heavy-duty rubber at its base wrapped around the stones on the edge of the quadrat. The animals in the quadrat were collected, to a depth of 10 cm, and immediately placed in 5% formalin. Two samples were taken at each station, and the animals identified to species where possible, and counted. Data from the two samples were then combined. Animals were collected from an estimated 1 m^3 of marginal vegetation, by sweeping a hand-net through the plants. The net had a mesh size of 0.6 mm. Two samples were taken at each station, and treated in the same way as the stony-bed samples.

Analysis of data

For each habitat, the relation between faunal samples was investigated using the Bray-Curtis similarity measure (Bray & Curtis 1957). In the analyses, all counts of animal abundance were log-transformed first. The resulting similarity matrices were summarised in two ways: by classification using group-average sorting (Lance & Williams 1967), with the results presented as a dendrogram in which similar samples clustered together; and by ordination using multidimensional scaling (Kruskal 1964), with the samples shown as points on a graph. Using the latter technique, similar samples are clustered together while dissimilar samples are

Table 1. Details of the eight sampling stations on the Eerste River.

Zone	Station number	Distance from source (km)	Altitude (m)	Other information
Mountain stream	1	2	382.3	Upstream from all human interference
Upper river	2	7	214.1	2 km below dam site
	3	12	152.9	
Lower River	4	20	76.5	Immediately below Stellenbosch
	5	22	68.8	
	6 & 7	23	64.2	Above and below sewage farm outfall respectively
	8	26	45.9	Downstream, the substrate changes to coarse sand

further apart. Each method distorts the relationship between samples to some extent, but the two together give a good indication of how robust the clusters are.

Distinct clusters of samples indicate the presence of relatively homogeneous assemblages of macroinvertebrates. While acknowledging that species changes in the biota along a river are usually transitional rather than abrupt, here, for clarity, the faunal assemblages have been treated as representative of separable animal communities in the river. With the communities identified and located, information statistic tests (Field 1969; Velimirov *et al.* 1977) were used to compare those that were spatial or temporal neighbours. Using the tests, species occurring statistically more frequently than expected in one of the two communities are revealed, and the species characteristic of each community thus established.

The correlation between the physical and chemical character of the water and the distribution of animal communities was investigated, using stepwise multiple discriminant analysis (Program BMD P7M, Dixon 1974). Before the analysis, the data for each environmental variable were standardised, using the formula (reading − mean)/(standard deviation); all values were thus expressed in standard deviation units. The water samples were then placed in groups according to the groups formed by cluster analysis of the faunal samples.

The analysis involves computing canonical discriminant functions between groups of water samples and plotting the first two functions to give an optimal two-dimensional picture of the separation of the groups. The resulting scatter diagram contains a multivariate centroid for each group, with the individual water samples indicated as surrounding points. The analysis also reveals the environmental variables which differ significantly ($P < 0.05$) among groups and produces a classification matrix, in which each water sample is placed in the group to which its probability of belonging is highest. The percentage of water samples in the matrix groups agreeing with the initial grouping of samples (based on the faunal relationships), indicates the degree of correlation between a named animal community and a stated set of environmental conditions.

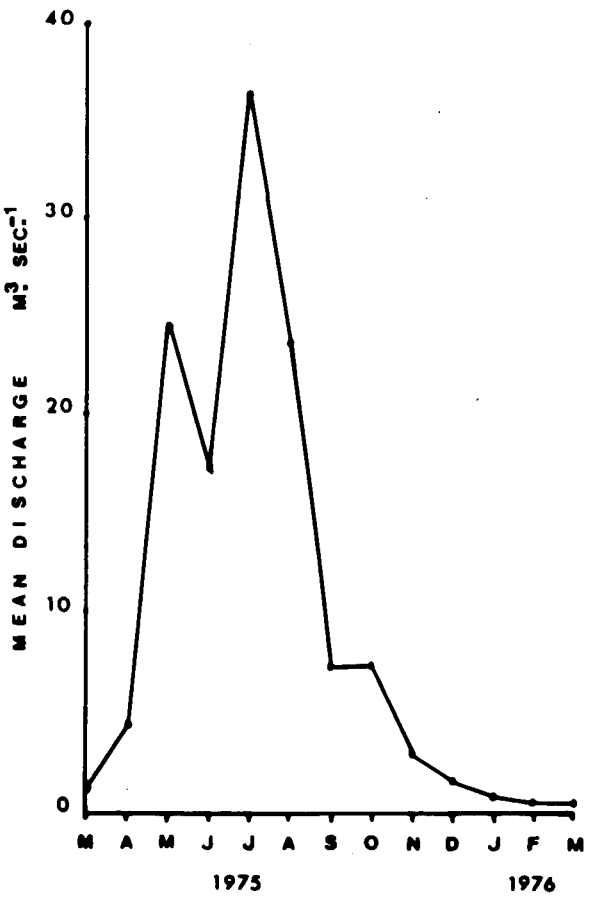

Fig. 2. Discharge of the Eerste River for the period of the survey. Data recorded by the South African Department of Forestry, at a weir below the dam site.

Results

Physical and chemical conditions

Discharge of the Mountain Stream (Fig. 2) was least between December and March (summer to early autumn) and greatest between May and August (late autumn to winter). Major spates occurred in May and July. The low summer discharge coincided with the maximum extraction of irrigation water for the surrounding vineyards and agricultural land.

Summer and winter changes of nine factors of water quality along the river are detailed in Appendix I. Dissolved oxygen levels were high throughout the study area in winter, though generally decreasing downstream (average of all stations:

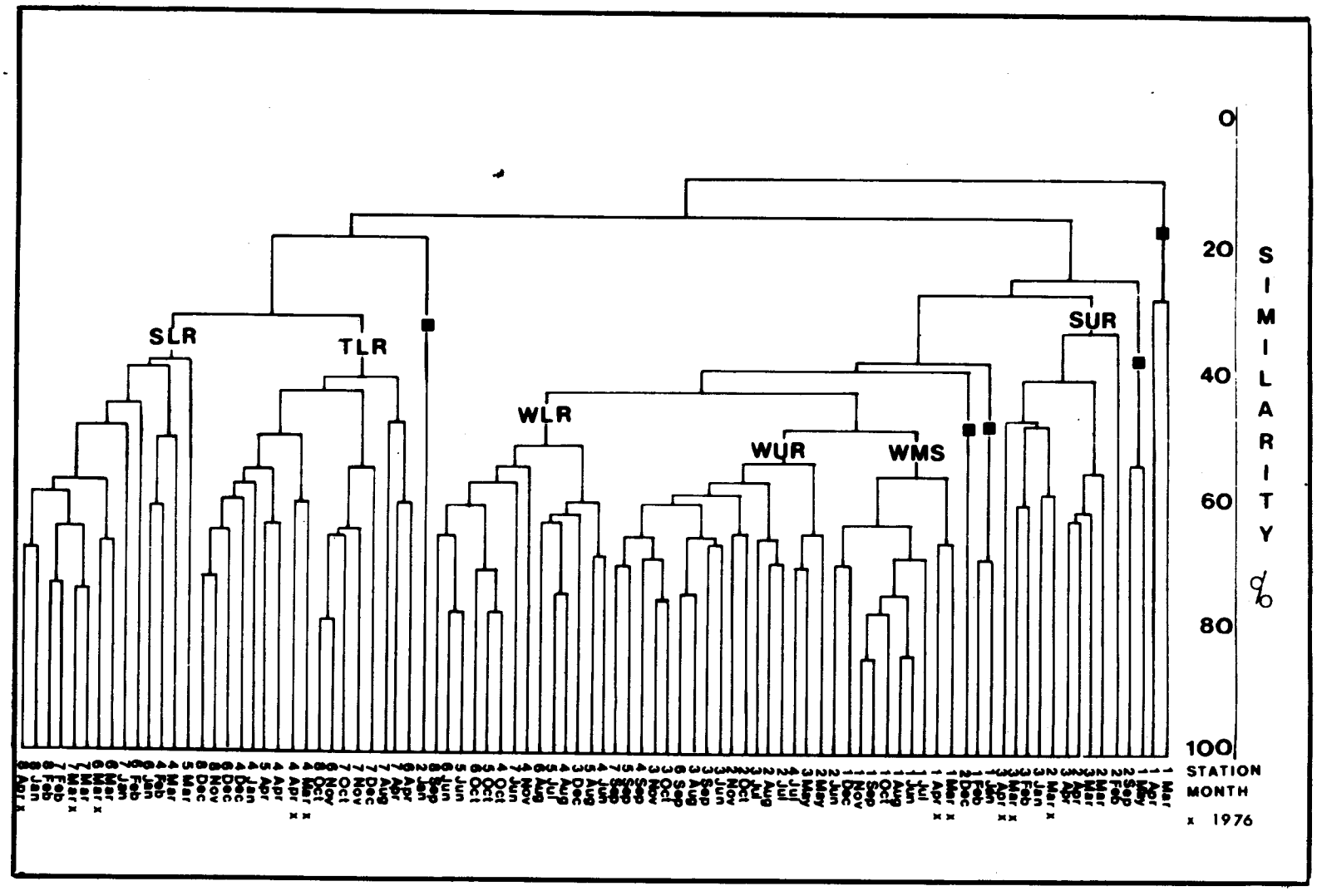

Fig. 3. Dendrogram showing the results of analysing faunal data from stony-bed samples. Clusters of samples represent separable faunal communities in the river. Communities: WMS – winter mountain stream; WUR – winter upper river; WLR – winter lower river; SUR – summer upper river; TLR – transitional lower river; SLR – summer lower river. ■ – samples not included in a community cluster.

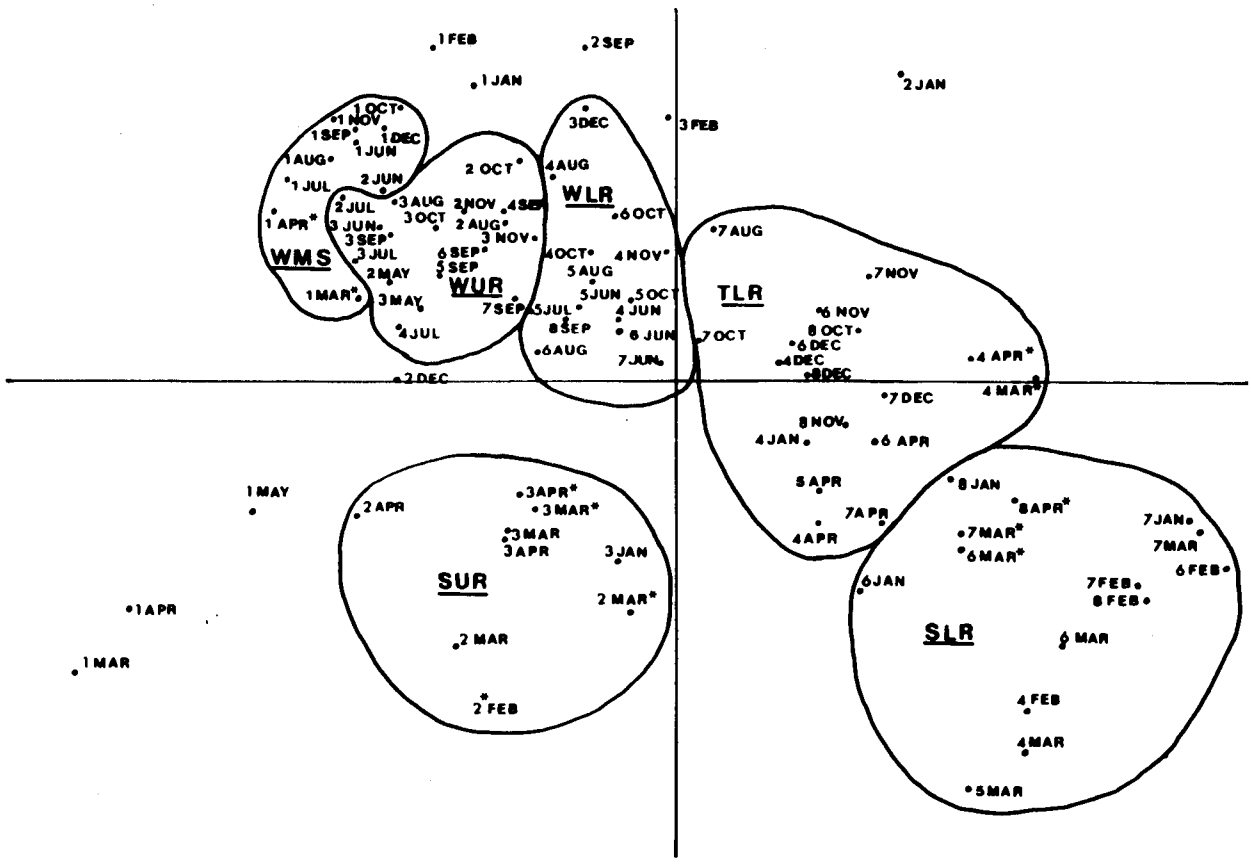

Fig. 4. Two-dimensional ordination showing results of analysing faunal data from stony-bed samples. Scales are arbitrary and arranged to minimise the distortion involved in reducing multidimensional data to two dimensions. Samples are identified as in Fig. 3, and grouped in the same way, except for 3 February which is now separated from SUR. Samples from March and April 1976 are starred; those from March and April 1975 unstarred.

9.7 mg ℓ^{-1}); the increase between stations 6 and 7 was due to turbulent flow through the sewage outlet. In summer, values decreased considerably downstream, particularly at Stellenbosch (station 4: 6.2 mg ℓ^{-1}) and at the sewage outfall (station 7: 4.2 mg ℓ^{-1}). The high summer levels at station 6 (8.0 mg ℓ^{-1}) were due to photosynthesising algae in stagnant pools.

Similar water temperatures were recorded throughout the study area in winter, with 10 °C and 14 °C the respective minimum and maximum daytime values. Temperatures along the river covered a greater range in summer: 18–21 °C were recorded at stations 1 and 2, and 23–28 °C at stations 3 to 8. pH levels were similar both seasons, and were usually just below neutrality in the Mountain Stream (6.3–6.8) and just above it in the two lower zones (7.0–7.6). In winter, current speeds were measured at least four days after a spate, and were similar at any one time throughout the study area (range 83–286 cm sec^{-1}). Summer speeds were much lower in all three zones (Mountain Stream and Upper River 15–54 cm sec^{-1}, Lower River 0–38 cm sec^{-1}).

Nitrite, nitrate and phosphate values increased from station 3 downstream, with station 7, below the sewage outfall, generally showing the highest levels. In the Lower River, winter levels of these three factors were sometimes higher than the summer ones, despite the greater volume of water; this was at least partially due to agricultural runoff and to incompletely treated sewage being pushed into the river by flood waters. The buffering capacity of the water (total alkalinity) increased downstream and was generally higher in summer than in winter. In both seasons, the highest values were recorded at station 7 (average 124.2 mg ℓ^{-1}). Steer (1964) reported a summer value of 12.5 mg ℓ^{-1} for the Mountain Stream. He concluded (1966) that though

the Mountain Stream was free of pollution and the Upper River 'reasonably clean', water quality of the Lower River deteriorated significantly during summer and autumn due to organic pollution and the poor flow. The deterioration continued until the advent of the winter rains. Though showing improvement in winter and spring, conditions deteriorated again each summer, in an annual repeating pattern.

The fauna of the stony bed

The dendrogram resulting from the analysis of stony-bed, faunal data shows that 91% of the samples fell into six main clusters (Fig. 3). In corroboration, the samples separated into the same six clusters, as a result of ordination (Fig. 4), with only one sample (station 3, February) failing to group in the same way as in Fig. 3. Multidimensional scaling revealed, however, that the groups were not as discrete as implied by the dendogram. The groups are considered to be representative of six separable animal communities in the river. These have been named the WMS (winter mountain stream), WUR (winter upper river), WLR (winter lower river), SUR (summer upper river), TLR (transitional lower river) and SLR (summer lower river) communities. In Fig. 4 the X-axis seems to separate the communities along the length of the river, while the Y-axis separates them seasonally.

A diagrammatic representation of the study area (Fig. 5) indicates the location of the six communities. Their distribution along the river divided it into three longitudinal, biotic zones. These coincided with the physical zones described above: the faunal community WMS was confined to the Mountain Stream zone, apart from a brief appearance in the Upper River (station 2) in June; WUR and SUR occurred only in the Upper River, apart from the appearance of WUR in the Lower River (station 4) in July, and again (stations 4–7) in September; WLR, TLR and SLR were characteristic of the Lower River.

The fauna of each zone exhibited different seasonal changes (Fig. 5). WMS was present in the Mountain Stream through most of the year, but was called a winter community because most of its fauna began new life cycles at the beginning of winter. In its absence (March, April, May 1975,

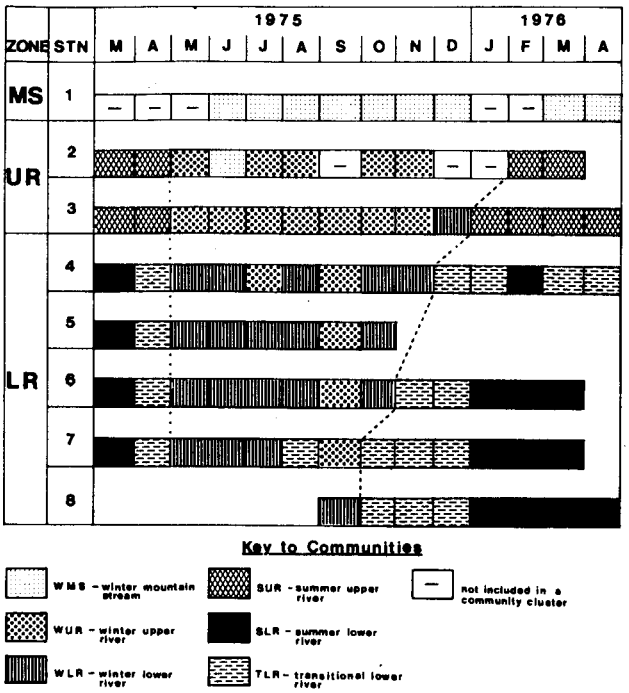

Fig. 5. The location of the six stony-bed communities in the river. The communities are those recognised in Figure 3. The vertical dotted and dashed lines show the appearance of winter and summer communities respectively, at stations 2–8. Zones: MS – mountain stream; UR – upper river; LR – lower river.

January, February 1976) samples from this stretch of river contained very few animals. WUR and SUR occurred in the Upper River in winter and summer respectively, with WUR present for about eight months of the year and SUR for four months. WLR and SLR appeared in the Lower River in winter and summer respectively, with WLR present for approximately six months and SLR for 3–4 months. A transitional community, TLR, occurred between WLR and SLR in both spring and autumn; it remained at station 4 for all but one month (February) of the dry season, but was confined to times of moderate flow (April, October, November, December 1975 – see Fig. 2) at lower stations. TLR has been treated as a summer community because it was more similar to SLR than to the other communities (Fig. 3), and because it occurred at station 4 through most of the summer.

The winter communities appeared almost simultaneously throughout the river as the winter rains began (May), while the switch back to the summer

Table 2. Results of information statistic tests of stony-bed samples, showing the species which differed significantly in frequency of occurrence between neighbouring communities. x = significant difference in frequency of occurrence at 5% level and xx at 1% level, in the compared communities

Species	Tests											
	Test number	1		2		3		4		5		6	
	Communities compared	WMS	WUR	WUR	WLR	WUR	SUR	WLR	TLR	TLR	SLR	SUR	SLR
	Number of samples	10	17	17	14	17	10	14	17	17	14	10	6
Cnidaria													
Hydra								0	6xx				
Turbellaria				3	10xx	3	8xx			15xx	6		
Hirudinea													
Glossiphonia disjuncta				1	8xx								
Mollusca													
Physa sp.										1	7xx	1	4x
Burnupia capensis				1	6x			6	17xx			0	5xx
Lymnaea columella												0	2x
Bulinus tropicus										2	7x	0	2x
Decapoda													
Potamon perlatus						2	7xx						
Ostracoda (1 sp.)								0	6xx	6	13xx	0	5xx
Ephemeroptera													
Aprionyx rubicundus		10xx	2										
Adenophlebia peringueyella		0	6x					7xx	1			7xx	0
Castanophlebia calida						17xx	2	14xx	5	5xx	0		
Choroterpes elegans				6xx	0	6x	0						
Baetis bellus				0	4xx	0	7xx					7xx	0
Baetis harrisoni										17xx	6	10xx	1
Acentrella capensis								11xx	2			7xx	0
Centroptilum sudafricanum								9xx	1			6xx	0
Centroptilum excisum						0	5xx	0	4x				
Pseudocloeon vinosum						0	5xx					5x	0
Cloeon lacunosum										1	10xx	0	5xx
Cloeon sp						0	2x						
Afronurus harrisoni						9	9x	3x	0			9xx	0
Austrocaenis sp.						3	8xx			8	12x		
Ephemerellina barnardi		8x	7	7xx	0	7xx	0						
Ephemerellina harrisoni						16xx	0	14xx	5	5xx	0		
Lestagella penicillata				16xx	3	16xx	2						

Trichoptera												
Athripsodes (bergensis group)			12xx	2	12xx	0						
Athripsodes sp. A					0	2x						
Athripsodes sp. B	2x	0										
Barbarochthon brunneum	2x	0										
Petrothrincus circularis					0	3x						
Cheumatopsyche spp.	5x	2										
Hydroptila capensis							0	3x				
Megaloptera												
Chloroniella peringueyi									3x	0		
Platychauloides sp.	6xx	1										
Plecoptera												
Aphanicerca spp.			16x	8	16xx	5	8xx	1			5x	0
Odonata												
Aeschna minuscula					2	5x						
Gerridae												
Gerris zuqualana									0	4xx	0	3xx
Corixidae												
Sigara contortuplicata									1	8xx	0	4xx
Micronecta scutellaris									3	9xx	0	4xx
Notonectidae												
Anisops varia scutellata									0	3x		
Coleoptera												
Hydrophilid larvae									0	3x		
Dytiscid larvae									0	11xx	0	4xx
Epidelmis capensis	10xx	4										
Ptilodactilidae (1 sp.)	8xx	1										
Helodidae larva A	4xx	0			0	2x						
Helodidae larva B	4xx	0										
Helodidae larva C	2x	0										
Rapnus sp.	3x	0										
Diptera												
Chironomus spp.							2	9x	9	12x	0	4xx
Rhagionidae	10x	13	13x	5			5x	1			5x	0
Blephariceridae	10xx	9			9xx	0	3x	0				
Tipulidae (1 sp - pupa)					5x	0			3x	0		
Unidentified larva (1 sp.)	0	7xx			7xx	0	5x	1				

communities occurred first at the lower stations and progressively later upstream (station 8 – October; station 6 – November; station 4 – December; station 3 – January; station 2 – February) (Fig. 5).

The six communities and the significant faunal differences between them (Table 2), are described below. More detailed information on the contribution of each species to the total macroinvertebrate numbers and standing crop will be given in a future publication.

a) WMS – the winter mountain stream community. WMS was dominated by insects (99.2% of the total invertebrate numbers). The Ephemeroptera, accounting for 37.9% of the numbers, consisted mainly of Leptophlebiidae and Ephemerellidae, with *Castanophlebia calida* and *Lestagella penicillata* the most abundant species. Blepharoceridae were numerous in the winter and spring (35.2%), while Trichoptera and Plecoptera were always poor in numbers (2.0% and 5.2% respectively) and in species. The Chironomidae, Rhagionidae and Simuliidae were continually present but not numerous (14.0% combined). Coleoptera of several typical mountain stream families – the Dryopidae, Elmidae, Hydraenidae and Helodidae – were present in small numbers (4.0%). Turbellaria, Oligochaeta and Decapoda were the only non-insect groups (0.8%).

b) WUR – the winter upper river community. Insects comprised 98.8% of the total invertebrate numbers. The Ephemeroptera were again well represented (74.8%), with *Baetis harrisoni, Castanophlebia calida, Lestagella penicillata* and *Ephemerellina harrisoni* the most abundant species. The proportional increase of Ephemeroptera from WMS to WUR was mainly due to the scarcity of Blepharoceridae in WUR. The Diptera as a whole accounted for only 19.1% of the numbers despite an increase in the Chironomidae. WUR had a lower proportion of Trichoptera (1.2%), Plecoptera (2.4%) and Coleoptera (0.7%), and a higher proportion of Oligochaeta (0.9%) than did WMS.

Significant faunal changes as WMS changed to WUR (Table 2, test 1) were the loss, or decreased frequency of several Ephemeroptera, including *Aprionyx rubicundus* and *Ephemerellina barnardi*, Trichoptera, including *Barbarochthon brunneum* and *Cheumatopsyche* spp., the megalopteran *Platychauloides* sp., the mountain-stream Coleoptera and the Blepharoceridae. Those species that were absent from WUR may be considered 'indicators' for WMS.

c) WLR – the winter lower river community. Insects comprised 76.1% of the total numbers, with the Ephemeroptera again the dominant group (53.9%). *Baetis harrisoni* and *Castanophlebia calida* were common species. Trichoptera, Plecoptera and Odonata were present but scarce, and individuals of other groups (e.g. the Hemiptera and Megaloptera) occurred occasionally. Dipteran numbers (19.6%) were mainly due to the Chironomidae; they included, at station 7, a few individuals of *Chironomus* spp. the local species group indicative of polluted or disturbed waters. Oligochaeta were the most abundant of the non-insects (20.3%), while the Hirudinea, Mollusca and Turbellaria were present but scarce.

Significant faunal changes as WUR changed to WLR (Table 2, test 2) were a further decrease in the Ephemeroptera, especially *Choroterpes elegans, Ephemerellina barnardi* and *Lestagella penicillata*, and in the Trichoptera, Plecoptera and Rhagionidae. Turbellaria, the hirudinean *Glossiphonia disjuncta*, the mollusc *Burnupia capensis* and *Baetis bellus* increased in frequency.

d) SUR – the summer upper river community. The proportion of insects (85.7%) was lower than in the corresponding winter community (WUR), with the Oligochaeta (10.7%) accounting for most of the increase in non-insect numbers. The Ephemeroptera were again numerous (59.3%), with *B. harrisoni* still abundant, but the other winter species rare. Characteristic summer species were *Afronurus harrisoni* (Heptageniidae), *Adenophlebia peringueyella* (Leptophlebiidae) and *Baetis bellus*. The latter normally occurs in marginal vegetation, but was forced down onto the river-bed by the falling water level. The Diptera (14.2%) consisted mainly of Chironomidae. Other groups were poorly represented: Trichoptera 7.0%, Plecoptera 0.7%, Coleoptera 2.2%.

Most of the significant faunal differences between SUR and WUR centred around the Ephemeroptera (Table 2, test 3), with the characteristic species of one community rare in, or absent from, the other. The winter community had a higher frequency of

Leptophlebiidae and Ephemerellidae, while the summer one contained mainly Baetidae, Heptageniidae and Caenidae. Other differences included a higher frequency of Turbellaria, and *Potamon perlatus,* and a lower frequency of *Athripsodes* (bergensis group) and *Aphanicerca* spp., in SUR.

e) TLR – the transitional lower river community. Insects comprised a larger part of the fauna (85.7%) than in the corresponding winter community (WLR), mainly because of a drop in the proportion of Oligochaeta (8.7%). The insects consisted almost entirely of Ephemeroptera (40.7%) and Diptera (44.9%), with the Trichoptera, Plecoptera, Megaloptera and Coleoptera virtually or completely absent. *B. harrisoni* accounted for about three-quarters of the ephemeropteran numbers, the remainder being remnants of the summer species (in autumn) and winter species (in spring). The high dipteran numbers were entirely due to Chironomidae and Simuliidae; these occurred in roughly equal numbers, and usually the numbers of one group were high when those of the other were low. *Chironomus* spp. was more frequent than in WLR. Non-insects, other than Oligochaeta, were present in similar proportions to WLR, with the additional presence of Ostracoda (1.1%) and *Hydra.* Though *Hydra* were usually scarce, a short-lived 'bloom' in November briefly raised their numbers to 5 600 m^{-2} and 74 000 m^{-2} at stations 6 and 7 respectively. Because of the brief life of these 'blooms' and the enormous numbers involved, *Hydra* has not been included in the above calculations of percentage composition.

TLR was the transitional community between the summer and winter ones in the Lower River, its fauna representing a halfway stage between the seasonal extremes. Significant faunal changes as WLR changed to TLR (Table 2, test 4) included a decrease in the winter ephemeropterans *Castanophlebia calida* and *Ephemerellina harrisoni* and of those species more typical of the upper river (*Acentrella capensis, Centroptilum sudafricanum, Afronurus harrisoni* and *Adenophlebia peringueyella*), and the appearance of the still-water species *Centroptilum excisum.* Other changes included an increased frequency of the mollusc *Burnupia capensis,* the algal-cased trichopteran *Hydroptila capensis* and *Chironomus* spp. plus the appearance of *Hydra* and the ostracods.

f) SLR – the summer lower river community. Insect numbers were at their lowest in SLR (55.7%) due to the virtual absence of the Ephemeroptera (3.7%). Those species present, *Cloeon lacunosum, Centroptilum excisum* and *Austrocaenis* sp. were rare and generally occurred only upstream of the sewage outfall. The Diptera (49.2%) consisted mainly of Chironomidae, with *Chironomus* spp. the most common species. Simuliidae were present but rare. The corixids *Sigara contortuplicata* and *Micronecta scutellaris,* and several different dytiscid larvae, comprised the remainder of the insect fauna (2.7%). Among the non-insects, the Ostracoda (26.5%), Mollusca (7.6%) and Hirudinea (2.6%) were more common than in TLR, while the proportion of Oligochaeta remained about the same. Though *Hydra* were rare, a second 'bloom' in January, at station 7 only, briefly raised their numbers to 44 700 m^{-2}.

As TLR changed to SLR (Table 2, test 5) there was a further loss of winter Ephemeroptera *(C. calida, B. harrisoni, E. harrisoni)* and a build-up of still-water species (*Cloeon lacunosum, Austrocaenis* sp.). The Corixidae, Gerridae and Notonectidae increased in frequency, as did the Mollusca, Ostracoda, hydrophilid and dytiscid Coleoptera and *Chironomus* spp.

The summer communities of the Upper (SUR) and Lower (SLR) Rivers were quite different (Table 2, test 6), with the characteristic species of one community usually completely absent from the other. While SUR was typified by a variety of Ephemeroptera, SLR contained mostly Ostracoda, Mollusca, Hemiptera, Dytiscidae and *Chironomus* spp.

Seven of the eight stony-bed samples excluded from community clusters (Figs. 3 & 4) were collected as one community was replacing another (Fig. 5). Their exclusion from the clusters was probably due to their low faunal numbers, and the consequent lack of information with which to classify them. The eighth sample (Sept. – station 2) was collected shortly after a heavy input of sediment into the river occurred between stations 1 and 2. Sediment blanketed the river bed at station 2 in September, and animals were scarce. In the same month, the faunal community WUR appeared at all stations downstream, except station 8 (Fig. 5). In the following months, faunal numbers remained

low at station 2 (hence the poorly recorded change-over from WUR to SUR), while the normal communities reappeared in the Lower River. WUR overshadowed WLR in the Lower River in September because the communities were similar and distinguished largely by a reduction of species as WUR changed to WLR. As the WUR fauna drifted downstream that month they made good the deficiency, briefly turning WLR to WUR.

The fauna of the marginal vegetation

Results of the cluster analyses of marginal-vegetation samples, using classification and ordination, are shown in Figures 6 and 7 respectively. The three broad clusters of samples in Fig. 6 are enclosed by boundary lines in Fig. 7.

Attempts to split the groups further were unsuccessful, as small clusters within the main ones in Fig. 6 were not necessarily mirrored by similar groupings in Fig. 7; when they were, their pattern of occurrence in the river often made no sense. The complex boundary lines in Fig. 7 indicate that even the three main groups of samples were not discrete.

To preserve continuity, the three communities have been named the MSV (mountain stream – vegetation), URV (upper river – vegetation) and LRV (lower river – vegetation) communities. The titles, however, indicate only the communities' main areas of occurrence (Fig. 8); for instance, three samples grouped in the mountain stream community were collected at stations 4, 6 and 7. Because of the broad grouping of samples, the marginal vegetation communities appeared to exist over larger temporal and spatial ranges than did comparable stony-bed communities. MSV was present at both stations 1 and 2, URV at stations 3 and 4 and LRV at stations 4 to 8. In the Mountain Stream and Upper River the marginal-vegetation habitat was only available when water levels were

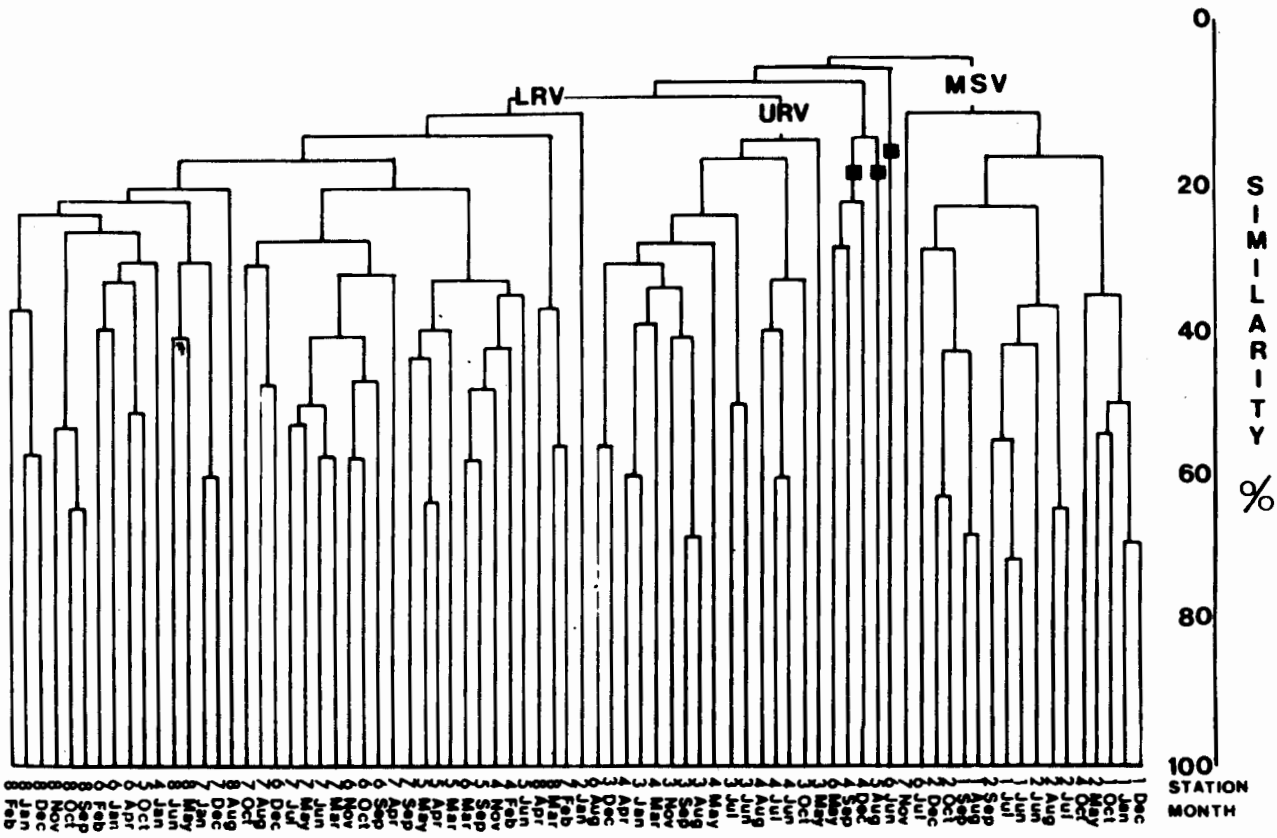

Fig. 6. Dendrogram showing the results of analysing faunal data from marginal-vegetation samples. Communities recognised: MSV – mountain stream (vegetation); URV – upper river (vegetation); LRV – lower river (vegetation). ■ -samples not included in a community cluster.

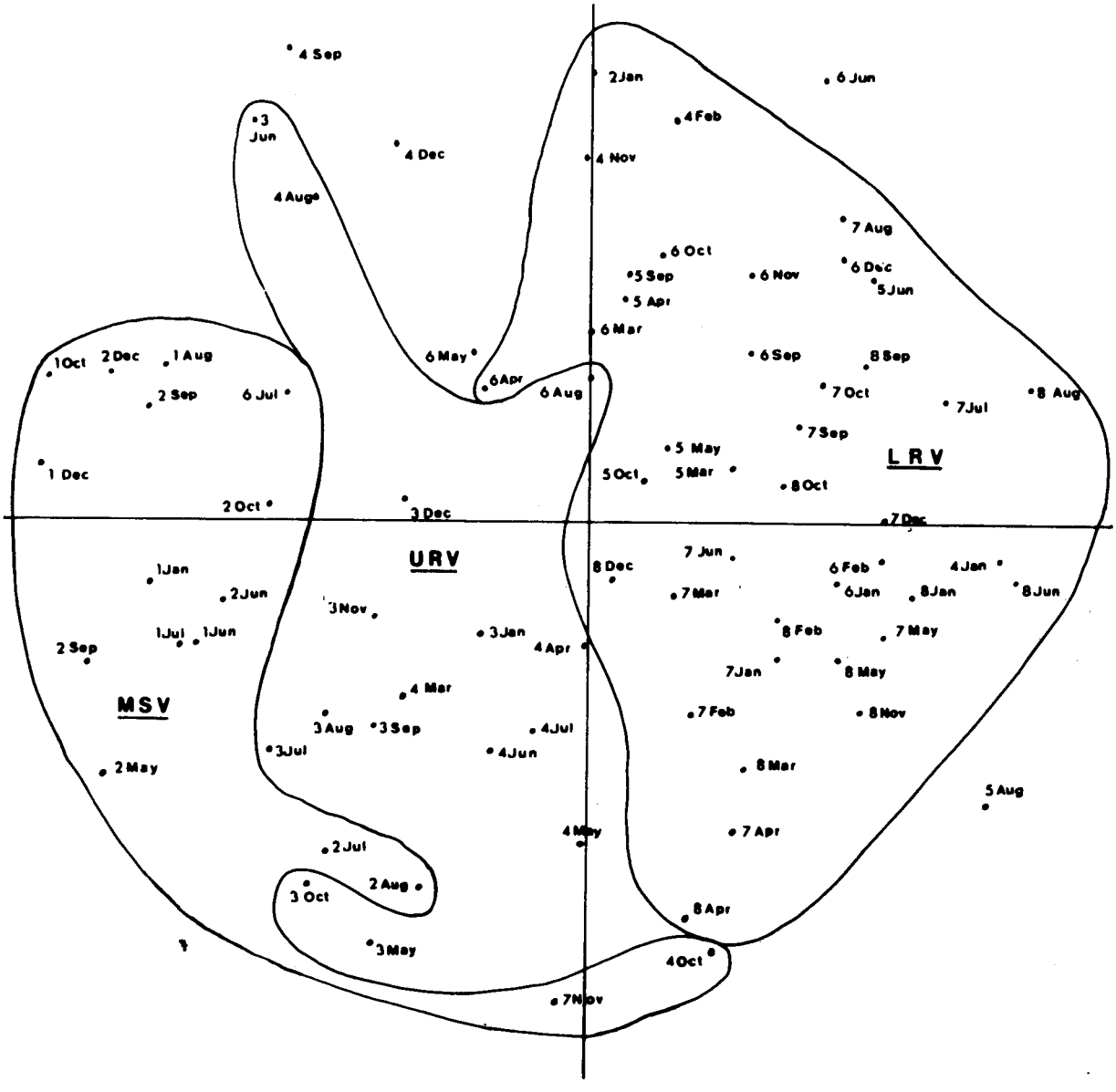

Fig. 7. Two-dimensional ordination showing results of analysing faunal data from marginal-vegetation samples. Samples are identified as in Fig. 6, and grouped in the same way.

high, and was always occupied by the same fauna, at any one station. In the Lower River the habitat was continually available, but seasonal changes did not show up in the cluster analyses. The three communities are described below. Because of the poor separation of samples into clusters, information statistic tests have not been applied to the data.

a) MSV – the mountain stream (vegetation) community. The community was dominated by insects (97.1%), with the different groups present in proportions similar to those in the corresponding stony-bed community, WMS. The Ephemeroptera (31.7%) and Diptera (36.3%) were most common, followed by the Trichoptera (15.9%), Plecoptera (5.7%), Coleoptera (4.6%) and Odonata (2.9%). Characteristic ephemeropterans were *Castanophlebia calida, Baetis harrisoni, Baetis bellus* and *Centroptilum sudafricanum*. The most common trichopterans were *Athripsodes* (bergensis group)

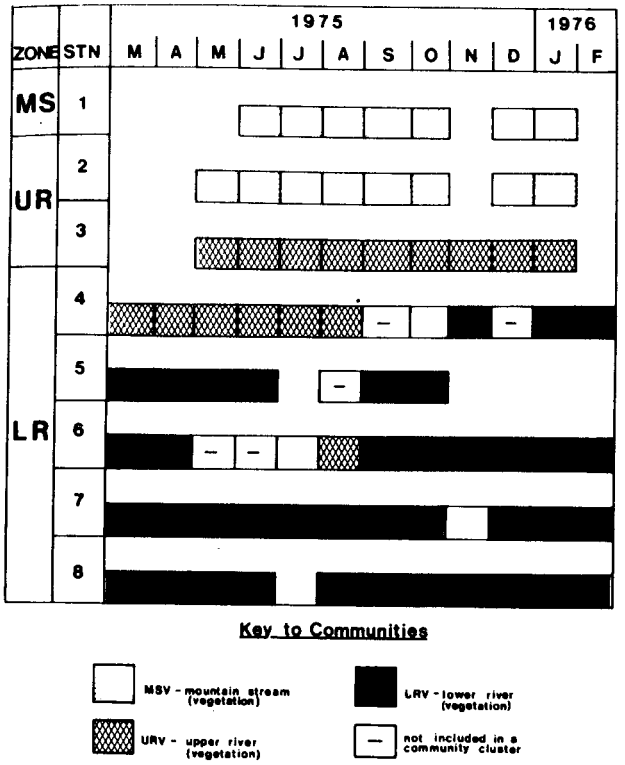

Fig. 8. Location of the three marginal-vegetation communities in the river. The communities are those recognised in Figure 6. Spaces left at stations 1–3 indicate periods when the water level was too low for a marginal-vegetation community to exist. Spaces at stations 5 and 8 in July indicate spoiled samples. Zones: MS – mountain stream; UR – upper river; LR – lower river.

and *Barbarochthon brunneum*, and odonate was *Pseudagrion salisburyense*. The Coleoptera were a mixture of Gyrinidae, Dytiscidae and the mountain-stream families (Elmidae, Helodidae, Hydraenidae, Dryopidae). Simuliidae and Chironomidae were the main dipterans, with occasional Rhagionidae, Culicidae, Tipulidae and Blepharoceridae. The non-insects (2.9%) were Turbellaria, Oligochaeta and, at station 2, a few weak-shelled molluscs.

b) URV – the upper river (vegetation) community. Insects accounted for 94.4% of the numbers. The Ephemeroptera were most common (51.2%) and included species typical of both summer and winter. The same species were present as in the corresponding stony-bed communities (WUR and SUR), but characteristic stony-bed species such as *Castanophlebia calida* and *Ephemerellina harrisoni* were less frequent, while *Centroptilum sudafricanum* and *Baetis bellus* were more common, especially at station 3. The same trichopterans, odonates and coleopterans were present as in MSV, with the exception of the mountain-stream Coleoptera. Those Hemiptera present (2.1%) were largely confined to station 4, and to the summer and autumn; they included *Gerris zuqualana, Rhagovelia infernalis africana, Sigara contortuplicata* and *Enithares sobria*. Chironomidae were the most common dipterans, with an occasional recording of *Chironomus* spp. at station 4. The non-insects (5.6%) included the winter and spring presence of Oligochaeta, and the summer and autumn presence of the hirudinean *Glossiphonia disjuncta* and the molluscs *Lymnaea columella, Burnupia capensis* and *Physa* sp.

c) LRV – the lower river (vegetation) community. As with the corresponding stony-bed communities, the proportion of insects was low (76.3%). The Ephemeroptera (22.4%) were mostly *Baetis harrisoni* and *Baetis bellus*, with some *Cloeon lacunosum* in summer; leptophlebiids were rare. The Diptera (49.1%) were mostly Chironomidae, with some Simuliidae at station 7. Other insects were rare: Trichoptera 0.6%, Odonata 0.8%, Hemiptera 2.3%, Coleoptera 1.0%. The non-insects (23.7%) were mainly Mollusca (13.1%), Ostracoda (6.2%) and Oligochaeta (2.8%).

The correlation between the physicochemical quality of the water and faunal distribution

Sixty-six water samples were complete, in that they contained a value for each of the variables dissolved oxygen (mg ℓ^{-1}), dissolved oxygen (percent saturation), pH, water temperature and current speed; of these, 54 also contained values for nitrite, nitrate, total phosphate and total alkalinity (no chemical analyses had been done for stations 1 or 2). The water samples were arranged according to the cluster-analysis groups of stony-bed faunal samples, and given the same six group names (WMS, WUR, WLR, SUR, TLR, SLR) with an additional 'W' to indicate 'water sample'. The stony-bed clusters were chosen in preference to those of the marginal vegetation because they were more distinct. Table 3 gives the mean values of the variables for each group of water samples (and thus

Table 3. Mean values and standard errors of the environmental variables for the six groups of water samples.

Variable		Group					
		WMSW	WURW	WLRW	SURW	TLRW	SLRW
Dissolved oxygen	Mean	9.14	8.82	8.18	7.86	6.95	5.20
mg ℓ^{-1}	Standard error	0.46	0.34	0.55	0.56	0.52	0.81
Dissolved oxygen	Mean	100.22	96.20	89.90	88.14	76.27	53.56
% saturation	Standard error	3.27	0.85	1.90	2.52	3.04	5.47
pH	Mean	6.7	7.0	7.7	7.1	7.4	7.3
	Standard error	0.2	0.1	0.2	0.1	0.1	0.2
Water °C	Mean	13.1	13.8	14.9	19.3	19.4	23.5
Temperature	Standard error	0.8	0.6	1.3	1.4	1.1	0.9
Current Speed	Range	34–154	35–286	30–189	4–36	4–157	0–35
cm sec^{-1}							
Nitrite	Mean	–	0.008	0.027	0.008	0.048	0.076
mg ℓ^{-1}	Standard error	–	0.001	0.012	0.002	0.021	0.038
Nitrate	Mean	–	0.091	0.329	0.089	0.744	0.210
mg ℓ^{-1}	Standard error	–	0.007	0.074	0.028	0.296	0.072
Total phosphate	Mean	–	0.463	1.648	0.547	1.800	3.098
mg ℓ^{-1}	Standard error	–	0.058	0.622	0.075	0.261	0.763
Total alkalinity	Mean	–	8.6	38.6	17.5	39.5	119.4
mg ℓ^{-1}	Standard error	–	1.1	17.4	4.4	5.9	15.7

for each stony-bed faunal community).

The discriminant analysis was initially performed on the 66 samples containing data on the five variables dissolved oxygen (mg ℓ^{-1}), dissolved oxygen (% saturation), pH, water temperature and current speed; these samples represented all sections of the study area (Table 3). The degree of agreement between the initial grouping of water samples (as based on the faunal clusters) and the grouping indicated in the discriminant analysis was 56.1% (Table 4). Distinctive groups (e.g. SURW) had a higher level of agreement than indistinct groups (TLRW). Most reclassifications involved placing a water sample in a group that was a neighbour in space or time. For instance, of the four samples reclassified from WMSW, two were placed in WURW and two in SURW. In the scatter diagram (Fig. 9) the groups of water samples blended one into another, as one would expect, considering the continual nature of the sampling medium. The group centroids were, however, in a logical sequence, with WMSW and SLRW at opposite extremes of the plot. Variables that differed significantly between the groups of water samples (and thus between the stony-bed communities), were dissolved oxygen (% saturation), pH and water temperature. Interpretation of the results is thus confined to these three variables. The groups were separated mainly on canonical variable 1, and formed a series of decreasing dissolved oxygen and increasing water temperature from the Mountain Stream (WMSW) to the Lower River in summer (SLRW); details are given in Table 3. Midwinter samples from the Mountain Stream (station 1: June – August) and late summer/autumn samples from the sewage outfall (station 7: February – March) predictably occurred at opposite extremes of the plot. The Mountain Stream (WMSW) and the Lower River in winter (WLRW) were separated from the other groups on canonical variable 2, and had the lowest (6.7) and highest (7.7) mean pH values respectively.

A second analysis was performed on the 54 samples containing data on nine environmental variables; added to the variables already analysed were nitrite, nitrate, total phosphate and total

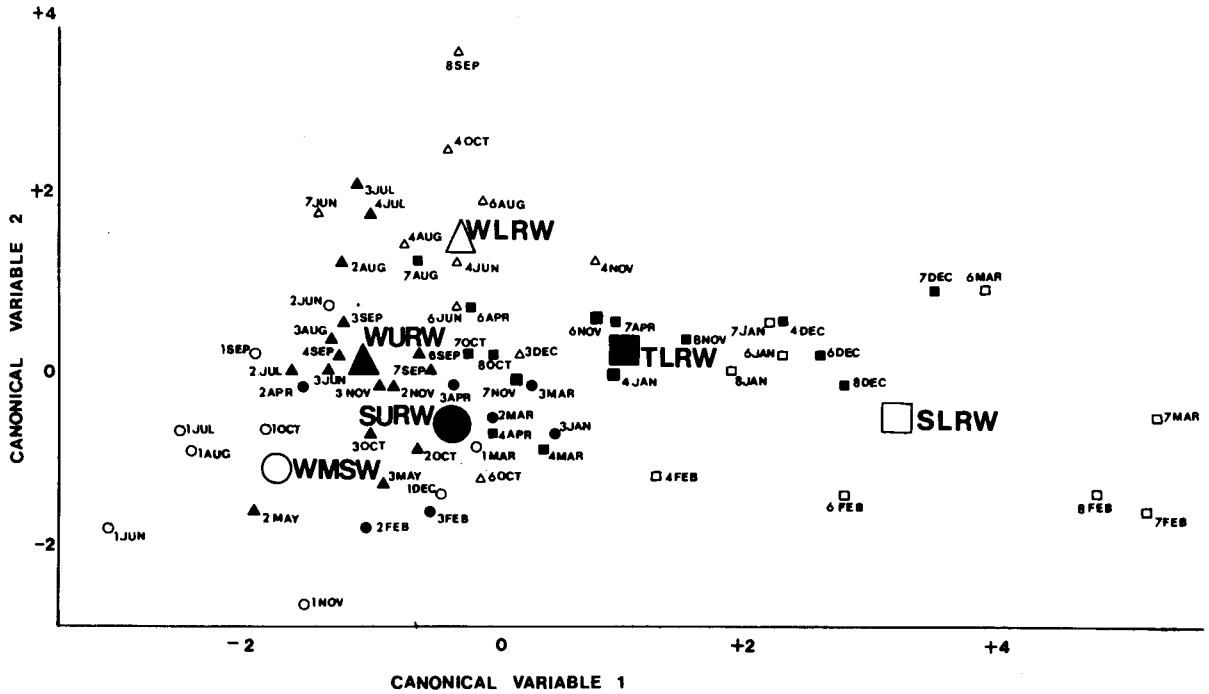

Fig. 9. Scatter diagram resulting from the stepwise, multiple discriminant analyses of 66 water samples, each of which contained data on five environmental variables. The water samples were pre-grouped according to the clusters of stony-bed samples (Fig. 3), and given the same group names, with an additional 'W' to denote water samples. The diagram is a two-dimensional picture of the separation of the groups. Large symbols - multivariate centroids of the groups. Small symbols - individual water samples, identified by station number and month of collection.

Table 4. Discriminant analysis classification matrix - all six groups of water samples, five variables.

Group	% Correct		Samples Reclassified					
			SLRW	TLRW	WLRW	WURW	SURW	WMSW
SLRW	55.6		5	3	0	0	1	0
TLRW	33.3		3	5	1	3	3	0
WLRW	70.0		0	0	7	1	2	0
WURW	50.0		0	0	2	8	3	3
SURW	100.0		0	0	0	0	7	0
WMSW	55.6		0	0	0	2	2	5
Mean	56.1	Total	8	8	10	14	18	8

alkalinity. WMSW was excluded from the analysis for lack of samples, and SURW represented by only four samples, from station 3. The initial grouping of water samples showed 79.6% agreement with the classification matrix (Table 5), with SURW again having the highest level of correspondence and TLRW the lowest. Pooling similar groups (SLRW with TLRW, WURW with WLRW) increased the agreeing classification to 87.3%.

Variables differing significantly between groups were dissolved oxygen (% saturation), total alkalinity and pH. In the scatter diagram (Fig. 10), the group centroids showed the same sequence as in Fig. 9. Horizontally (canonical variable 1), the groups formed a series of decreasing dissolved oxygen and increasing total alkalinity from the Upper River in winter (WURW) to the Lower River in summer (SLRW). Vertically (canonical variable

Table 5. Discriminant analysis classification matrix – five groups of water samples, nine variables.

Group	% Correct		Samples reclassified				
			SLRW	TLRW	WLRW	WURW	SURW
SLRW	88.9		8	1	0	0	0
TLRW	66.7		0	10	1	0	4
WLRW	70.0		0	0	7	0	3
WURW	87.5		0	0	2	14	0
SURW	100.0		0	0	0	0	4
Mean	79.6	Total	8	11	10	14	11

2), the Lower River in winter (WLRW) was again separated from the other groups, and had a higher value for pH.

Discussion

The aquatic macroinvertebrates of the Eerste River undergo spatial and temporal changes in their species composition (Figs. 5 and 8). These changes are predictable, in that the same group of species occurs in the same season and place each year (pers. obs. in years following original survey). Such phenomena are by now well documented. Among those who have described longitudinal and/or seasonal changes in the species of lotic macroinvertebrates are: Harrison & Elsworth (1958), Chutter (1963), Hynes (1961, 1968, 1970), Harrison (1965), Egglishaw & MacKay (1967), Minshall (1968), MacKay (1969), MacKay & Kalff (1969), Bishop (1975), Minshall & Minshall (1978), Andrews & Minshall (1979a, 1979b), Towns (1979) and Gore (1980). Often the described changes have been based on differences between pooled groups of

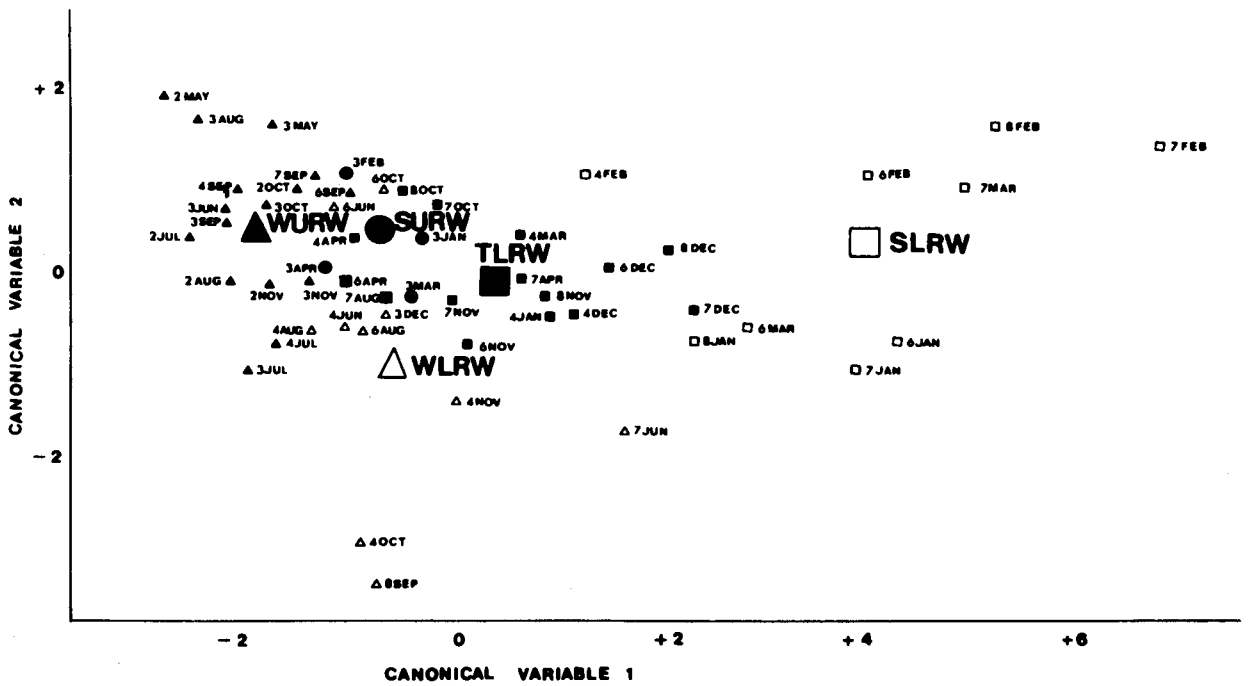

Fig. 10. Scatter diagram resulting from the stepwise multiple discriminant analysis of 54 water samples, each containing data on nine environmental variables. Pre-grouping and identification of samples as in Fig. 9.

faunal samples, each group representing a preconceived 'zone' or 'season' in the river. In this investigation, through cluster analysis of the faunal samples, the fauna themselves have pinpointed the times and places of their changes in community structure.

The analyses indicated that the stony-bed communities were more limited in distribution than the marginal-vegetation ones (Figs. 5 & 8). Kemp *et al.* (1976) found the marginal vegetation fauna less satisfactory to classify than the stony-bed fauna, and attributed this to the greater variability of the marginal-vegetation habitat. Chandler (1970) concluded that animals from the stony-bed habitat were most useful for pollutional studies, as they were most sensitive to changes in their environment.

Further discussion below has been confined to the stony-bed communities, because of their clear distribution pattern in the river.

Three biotic zones, each with a distinctly different fauna, were identified in the study area (Fig. 5). The biotic zones corresponded to obvious physical zones. In terms of Illies' (1961) system of river zonation, the Mountain Stream was equivalent to the upper rhithron, the Upper River to the lower rhithron and the Lower River to the upper potamon. Harrison (1965) recognised these and others of Illies' zones in several southern African rivers.

Seasonal changes in the fauna differed in the three zones (Fig. 5). In the Mountain Stream, the single, year-long community (WMS) was dominated by insects, which first appeared in late autumn/early winter, and grew slowly to emerge as winged adults in summer. In 1976, WMS appeared earlier (March) than in 1975 (June), and contained smaller animals (unpublished data). Possibly the young animals begin their life cycles deep in the substrate sometime before appearing at the substrate surface (see Coleman and Hynes (1970) for discussion on vertical migration of benthic fauna down into the river-bed), and thus are smaller the earlier they migrate upwards. Very few animals were found in the months between successive WMS communities (March - May, 1975; January - February, 1976); those present were late-maturing remnants of the old community, and some individuals of the ephemeropteran *Aprionyx peterseni*. Hynes (1970) states that if, after the winter species have emerged, the remaining summer season is too short for a species to complete its life cycle, it will not occur. The brief gaps between WMS communities appear to be unsuitable for the establishment of a summer community.

In the Upper River, the winter community (WUR) was present twice as long (8 months) as the summer one (SUR 4 months). The two communities were quite different in species structure, though both contained a high percentage of insects. In both, numbers were initially high, as eggs hatched, and finally low, as animals emerged as winged adults. Hynes (1970) describes such a pattern for streams dominated by insects.

Of the three winter communities, the one in the Lower River, WLR, was present the shortest time (5–7 months). WLR had a high percentage of insects and, as with the Upper River communities, faunal numbers were initially high and finally low. The summer community, SLR, was present for 3–4 months. Non-insects, especially ostracods and molluscs, were abundant in SLR, and total animal numbers continued to increase until the winter rains began. Hynes (1970) describes this pattern as typical of streams dominated by multivoltine snails or Peracarida. TLR, the transitional community, occupied the Lower River for the remaining months of the year, occurring both in spring and in autumn. Its species composition was intermediate between the extremes of WLR and SLR. The summer build-up of molluscs, ostracods, *Chironomus* spp. and others began when TLR appeared in spring, and the last remnants of these species were in TLR when it reappeared at the time of the first light rains. Similarly, winter species were present as late-maturing individuals in spring, and as newly-hatched larvae and nymphs in autumn. Where TLR did not give way to SLR, but remained through the summer (station 4), the fauna was characterised by a lower concentration of the summer species present at stations 6–8, and a higher concentration of still-water ephemeropterans.

The trend through the study area was of winter communities occupying the stony-bed habitat longer, the nearer they occurred to the source of the river. As these communities disappeared, summer communities replaced them where possible. The Mountain Stream supported only the winter community each year, while both the Upper and Lower Rivers supported summer and winter ones. Because of the different durations of the winter communi-

ties, the summer community of the Lower River was present longer than that of the Upper River. (TLR was not a third community being squeezed into the Lower River, but a summer community that would have persisted there if the physico-chemical environment had not deteriorated so drastically.) The three winter communities shared several common, univoltine species whose aquatic lives were as long as the duration of their respective communities (unpublished data). Animals of the same winter species were thus present longer in, and emerged later from, the Mountain Stream than the Lower River. Additionally animals from the Mountain Stream were smallest at emergence, while those from the Lower River were largest. These different levels of secondary productivity along the river will be the subject of a subsequent paper.

The three winter communities (WMS, WUR, WLR) were similar, while the summer ones above (SUR) and below (TLR, SLR) Stellenbosch were quite dissimilar (Figs. 3 and 4). SUR, with its high proportion of insects, resembled the winter communities more than TLR and SLR. These faunal associations were reflected in the associations of the water samples, which can be 'visually judged' (Green & Vascotto 1978) in Figs. 9 and 10; Table 3 indicates the reasons for the similarity. The physicochemical quality of the water was more uniform through the study area in winter than in summer. For instance, mean water temperature between the Mountain Stream and the Lower River increased by only 1.8 °C in winter, but by 10.4 °C in summer. Mean dissolved oxygen (% saturation) showed a corresponding downstream decrease of 10.3% in winter and 46.7% in summer. The Upper River was above the major sources of pollution, and thus did not exhibit the same summer deterioration in water quality as the Lower River. Values of some environmental variables for the Upper River in summer (e.g. dissolved oxygen, water temperature) were more extreme than for any winter sample, while values of other variables (e.g. pH, nitrite, nitrate, phosphates) were similar to those for the Upper River in winter. This was reflected in the positioning of SURW near to, but to one side of, the winter groups of water samples in the scatter diagrams (Figs. 9 & 10).

Discriminant analyses revealed that the variables differing significantly between groups of water samples (and thus between stony-bed faunal communities) were dissolved oxygen (% saturation), water temperature, pH and total alkalinity. The over-riding importance of dissolved oxygen, and to a lesser extent of the allied variable water temperature, can be appreciated when noting that levels of the nutrients nitrite, nitrate and phosphate were sometimes higher in winter than in summer (details in Appendix I), yet the winter fauna did not show the same drastic, downstream changes in species composition as the summer fauna. The cold, turbulent winter flow presumably maintained a sufficiently high dissolved oxygen level for the winter fauna to cope with organic pollutants without undergoing such a complete change of species. Total alkalinity and pH, both of which showed increased values downstream, may have been influencing factors in the establishment of the three biotic zones.

Grouping of water samples, based on the clustering of faunal samples, appears to have considerable validity (Tables 4 & 5). Depending on the number of variables included in the discriminant analysis, 56.1% (5 variables) or 79.6% (9 variables) of the water samples were correctly grouped in this way. Reclassified samples were usually placed in a group that was a spatial or temporal neighbour. For instance, the sample reclassified from SLRW to TLRW (Table 5) was collected at station 4 in February 1976. Fig. 5 shows that TLR was in fact the prevalent faunal community at station 4 throughout that summer. Similarly, of the two samples reclassified from WURW to WLRW (Table 5) one was collected at station 4 in July 1976. As suggested by the reclassification, the faunal community WLR normally occurred at station 4, but had been replaced by WUR that one month (Fig. 5).

In both the above examples, the fauna changed briefly, while the water samples remained similar to others taken at the same place and time of year. There are a number of possible explanations for this, including high sensitivity of the fauna to small environmental changes and reaction of the fauna to environmental changes which were not monitored. The high level of agreement between groups of faunal samples and groups of water samples, however, indicates that environmental changes are usually quickly reflected by changes in the species composition of the fauna. While acknowledging that a much wider range of chemical analyses would be necessary to establish the predictive value of this

relationship, the results do indicate a strong correlation between faunal distribution and the physical and chemical quality of the water.

In conclusion I feel that hydrobiological studies of rivers such as the Eerste River, with their miniature zones and simple profiles, can advance our understanding of rivers in general. Longitudinal changes in their macroinvertebrate fauna would probably be simple, one-way trends in such factors as species composition and secondary productivity, and relatively few samples would be necessary to monitor such changes. A more limited number of external factors would be implicated in the trends than in longer and more complex river systems. The spatial and temporal distribution pattern of the macroinvertebrates of the Eerste River clearly revealed their reactions to the seasonal cycle and the changing physicochemical quality of the water along the river. This information will provide a valuable base-line when monitoring future changes in the river, especially those following the completion of the Jonkershoek dam.

Summary and conclusions

1. Faunal samples collected from the stony-bed and marginal-vegetation habitats of the stony-bed section (upper 26 km) of a small (40 km) South African river, were used to investigate spatial and temporal changes in the species composition of the macroinvertebrates. Cluster analyses of the samples revealed the presence of assemblages of invertebrates, which were treated as representative of separable animal communities in the river.

2. Stony-bed communities were found to be more clearly and restrictively distributed than marginal-vegetation communities, and further discussion was confined to the former.

3. Spatial distribution of the stony-bed communities divided the river into three, longitudinal biotic zones, which corresponded with obvious physical zones: the Mountain Stream (7 km), Upper River (5 km) and Lower River (14 km) zones.

4. Temporal changes in the species composition of the fauna were different in the three zones. In the Mountain Stream a slow-growing, insect-dominated community appeared at the beginning of winter and took approximately one year to grow to maturity. It was then replaced by another similar community. In the Upper River, winter and summer communities alternated, occupying the habitat for eight months and four months respectively. The two communities had different species compositions, but both were dominated by insects. Winter and summer communities, each lasting roughly six months, also occurred in the Lower River. While the winter community was similar in species composition to the winter ones of the two higher zones, the summer community had a high percentage of non-insects, particularly molluscs and ostracods. The trend through the study area was of winter communities persisting longer, the closer they occurred to the source of the river; as they disappeared, summer communities replaced them where time allowed.

5. There were downstream changes in the physical and chemical quality of the water. While the Mountain Stream was free of pollution and the Upper River 'reasonably clean', water quality of the Lower River fluctuated from 'poor' in the summer (low dissolved oxygen and flow, high water temperature and nutrient levels) to 'improved' in the winter (high dissolved oxygen and flow, low water temperature, but still occasional high nutrient levels). The annual deterioration of the Lower River was mainly due to poor summer flow, combined with the continued input of organic effluents from Stellenbosch.

6. Correlations between changes in the physical and chemical quality of the water and changes in the faunal communities were investigated using multiple discriminant analysis. The results indicated a strong correlation between the two. Environmental variables that differed significantly between faunal communities were dissolved oxygen, water temperature, pH and total alkalinity.

7. I conclude that studies of short rivers with simple profiles, such as the Eerste River, can advance our understanding of rivers in general. The distribution pattern of macroinvertebrates in the Eerste River, and its relation to changes in the physicochemical quality of the water, provide base-line information for monitoring future changes in the river's ecology.

Acknowledgements

My sincere thanks to Drs G. Branch, T. Crowe, B. Davies, J. Day, J. Field and R. Siegfried, for

Variable	Zone:	Mountain Stream		Upper River				Lower River							
	Station:	1		2		3		4		6		7		8	
		S	W	S	W	S	W	S	W	S	W	S	W	S	W
Dissolved Oxygen	Mean	8.4	11.2	8.3	10.1	8.3	9.9	6.2	9.4	8.0	8.6	4.2	9.2	4.7	–
mg ℓ^{-1}	Standard error	0.1	0.3	0.1	0.1	0.3	0.4	0.5	0.2	1.6	0.4	0.8	0.2	0.7	–
Dissolved Oxygen	Mean	94.2	102.5	93.7	99.0	93.2	95.5	72.4	95.0	91.6	88.0	49.9	93.5	54.9	–
Percent saturation	Standard error	0.5	3.7	0.3	0.8	0.7	1.2	3.7	1.6	17.4	2.4	10.2	2.8	9.0	
pH	Mean	6.8	6.3	7.2	7.2	7.2	7.0	7.3	7.6	7.4	7.4	7.5	7.6	7.6	–
	Standard error	0.1	0.1	0.3	0.1	0.2	0.4	0.3	0.1	0.2	0.2	0.4	0.2	0.1	–
Water temperature	Mean	19.7	11.0	20.2	11.7	21.8	11.7	25.7	11.5	25.5	12.2	24.3	12.3	24.5	–
°C	Standard error	0.7	0.3	0.9	1.2	0.9	1.2	0.8	0.3	1.8	0.6	0.9	0.7	0.8	–
Current Speed															
cm sec^{-1}	Range	20–54	116–167	15–33	83–185	18–28	125–286	0–24	102–177	0–15	124–189	5–38	108–286	4–35	–
Nitrite	Mean	–	–	–	–	0.005	0.010	0.012	0.011	0.015	0.042	0.193	0.108	0.160	0.059
mg ℓ^{-1}	Standard error	–	–	–	–	0.002	0.001	0.005	0.001	0.008	0.029	0.076	0.038	0.055	0.012
Nitrate	Mean	–	–	–	–	0.165	0.119	0.122	0.291	0.178	0.394	0.552	0.825	1.010	0.728
mg ℓ^{-1}	Standard error	–	–	–	–	0.038	0.024	0.025	0.076	0.107	0.060	0.144	0.517	0.860	0.179
Total Phosphate	Mean	–	–	–	–	0.680	0.482	1.000	0.801	4.707	1.241	3.040	3.510	1.773	1.162
mg ℓ^{-1}	Standard error	–	–	–	–	0.040	0.185	0.200	0.100	1.449	0.193	1.388	1.781	0.542	0.319
Total alkalinity	Mean	–	–	–	–	20.00	7.66	54.33	18.33	109.00	18.33	123.33	125.00	90.67	33.30
mg ℓ^{-1}	Standard error	–	–	–	–	2.89	2.67	19.54	1.67	44.09	1.67	48.08	40.41	23.35	7.26

Appendix I. Summer (S) and Winter (W) values of nine factors of water quality, along the river. Mean values and standard errors are given, except for 'current speed' where the range is shown. Measurements of current speed were taken at least four days after a spate.

critically reviewing various drafts of the paper. The following specialists kindly verified faunal identifications: J. D. Agnew (Ephemeroptera), H. Bertrand (Coleoptera), M. W. Mansell (Megaloptera), J. Omer-Cooper (Dytiscidae), J. H. Oosthuizen (Hirudinea), F. de Sallier Dupin (Hemiptera), K. M. F. Scott (Trichoptera) and B. C. Wilmot (Odonata).

The research was supported financially by the Council for Scientific and Industrial Research, and the University of Cape Town. The S.A. Department of Forestry allowed me to work in the Jonkershoek Nature Reserve.

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Received September 11, 1980.

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PART 2

ABUNDANCE, BIOMASS AND DIVERSITY OF BENTHIC MACRO-INVERTEBRATES IN A WESTERN CAPE RIVER, SOUTH AFRICA

Trans. roy. Soc. S. Afr. (in press)

ABSTRACT

The Eerste River is situated in the south-western Cape Province, South Africa. Its upper reaches have a stony substratum, and can be divided into three physical/biotic zones: The Mountain Stream, Upper River and Lower River zones. Investigations of the abundance, biomass, species diversity and species composition of the benthic macro-invertebrates in the three zones were carried out in 1975/76. Spatial and temporal changes in these factors can be correlated with changes in the physico-chemical quality of the water. Abundance and biomass generally increased downstream, but were low below a dam construction-site, because of the blanketing effects of silt on the substratum. Seasonal changes in abundance and biomass differed in the three zones, but always included a peak in spring. The highest values of both were in the Lower River in summer, reflecting the build-up of organic pollutants there during times of low flow. Diversity of the Ephemeroptera, which was felt to be representative of a change in diversity of the fauna as a whole, generally decreased downstream, with a major drop at the town of Stellenbosch, and another at a sewage-farm outfall. A misleading increase in diversity occurred, however, in the silt-laden waters below the dam site, due to the fleeting occurrence of individuals of several different species. Composition of the fauna was typical of local rivers with mountain sources. Figures for abundance, biomass and calorific values of species are given in appendices.

INTRODUCTION

Hydrobiological studies of South African rivers have dealt primarily with the physico-chemical character of the waters and the distribution and abundance of the aquatic biota (see King, 1981). There is some information on the biology and life histories of riverine invertebrates (e.g. Chutter, 1961; Chutter, 1968; Chutter, 1972a; Noble, 1970) while Chutter (1972b) has dealt with the species diversity of aquatic invertebrates in connection with proposed biotic indices of the quality of water in South African rivers and streams. There is no published information on the total biomass of macro-invertebrates in any South African river.

The Eerste River is a small river in the south-western Cape Province. The spatial and temporal distribution of aquatic macro-invertebrate communities of its stony-bed habitat has been described (King, 1981 and see Table 1). Changes from one community to another occurred in response to the seasonal cycle and to downstream changes in the river's physico-chemical character. Data on abundance, biomass, species diversity and species composition of the macro-invertebrates are presented in this paper and interpreted in the light of the earlier findings.

THE STUDY AREA

The Eerste River rises in the Dwarsberg Mountains, 60km east of Cape Town, and is 40 km long (Fig. 1). Its catchment (400 km^2) lies entirely within the winter rainfall area of South Africa. Yearly

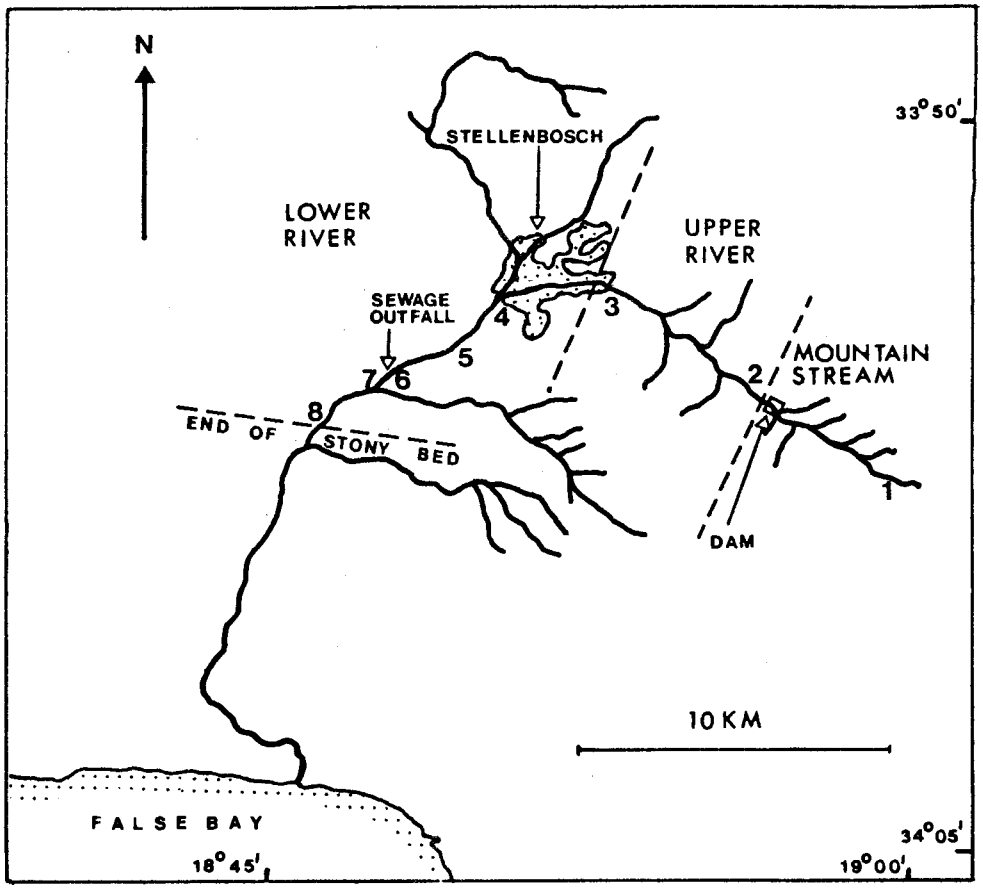

Fig. 1 The Eerste River , showing the three physical/biotic zones within the study area, and the eight sampling stations.

rainfall ranges from 3000 mm on the mountains to 700 mm or less on the coastal plain. Discharge during the study, measured 6 km downstream from the source of the river, ranged from a maximum of 36,5 cumecs in winter, to a minimum of 0,33 cumecs in summer. The river is usually less than 1m deep, but is subject to winter spates.

The study area comprised the upper 26 km of the river, this being the extent of the stony substratum (Fig. 1). The three physical/biotic zones within this area - the Mountain Stream, Upper River and Lower River - are described by King (1981) and the salient features are repeated in Table 1. Two major influences on the river's ecology were the presence of a dam construction-site at the lower end of the Mountain Stream, and the town of Stellenbosch at the junction of the Upper and Lower Rivers. Construction of the dam began shortly before the start of this study, and turbidity of the water below the site increased noticeably during the study (unpublished data). Stellenbosch has no heavy industry, but winery, sewage and other effluents enter the Lower River, via a sewage treatment plant and elsewhere, resulting in a rapid deterioration in water quality there at times of low flow.

METHODS

Faunal samples were collected at monthly intervals between March 1975 and April 1976, from eight stations along the river (Fig. 1). Further details of their location are given in Table 2. Station 5 was abandoned in October 1975 due to its similarity to stations 4 and 6, and station 8 was created in September 1975, in order to investigate recovery of the

Table 1. Physical, chemical and biotic features of the three zones of the study area during the study period. The invertebrate communities listed are described briefly in the text and more fully by King (1981).

Feature	Mountain Stream	Upper River	Lower River
Length (km)	7	5	14
Width (m)	5 - 7	7 - 11	8 - 18
Gradient ($m\ km^{-1}$)	24	12	2
Substratum	boulders, large stones, bedrock	boulders, large and small stones	large and small stones on coarse sand
Dissolved oxygen (% saturation)	87 - 113	83 - 107	30 - 113
Water Temp. °C	10 - 21	10 - 26	11 - 28
pH	5,8 - 7,1	6,4 - 7,7	6,8 - 8,8
Nutrient levels (NO_2 NO_3 PO_4)	negligible	low	high
Riparian vegetation	small, indigenous evergreen trees e.g. *Metrosideros angustifolia* *Brabejum stellatifolium*	*Quercus robur* gradually replaces indigenous trees	mixed evergreen and deciduous trees
Land use in catchment	**fynbos and plantations of *Pinus radiata*	vineyards	agricultural land orchards vineyards
Semi-submerged marginal vegetation	sparse - mostly *Prionium serratum*	sparse - mostly *Prionium serratum*	abundant - mostly grasses
Benthic invertebrate communities present	WMS - the winter mountain stream community	WUR - the winter upper river community SUR - the summer upper river community	WLR - the winter lower river community TLR - the transitional lower river community SLR - the summer lower river community

**Fynbos = indigenous sclerophyllous vegetation of the southern and south-western Cape Province

Table 2. Location of the eight sampling stations in the study area

Lower River (i) is above the sewage-plant outfall

(ii) is at the outfall

(iii) is 3 km downstream from the outfall

Zone	Sub-zone	Sampling Station	Distance from source (km)	Altitude (m)	Remarks
Mountain Stream	-	1	2	382,3	Above all human interference
Upper River	-	2	7	214,1	2km below dam site
		3	12	152,9	Immediately above Stellenbosch
Lower River	(i)	4	20	76,5	Immediately below Stellenbosch
	(i)	5	22	68,8	
	(i)	6	23	64,2	
	(ii)	7	23	64,2	
	(iii)	8	26	45,9	End of stony bed

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river from the sewage effluent. Below station 8 the substratum changes from stones to sand, precluding study by the same methods.

The equipment used for sampling the stony-bed habitat is described in King (1981). Briefly, 0,25m^2 of river bed was sampled to a depth of 10 cm, using apparatus that incorporated a net of 0,6mm mesh size. This retained animals down to 1 mm size. Two samples per month were collected at each station, and preserved with 5% formaldehyde. Animals were identified to species where possible, counted and dried to constant weight at 60° C to obtain biomass data. Mollusc shells were decalcified first in nitric acid. Data from the pair of samples collected at the same place and time were then pooled. After weighing, the dried animals were stored for later calorific analyses. Calorific values of species were determined using a Phillipson microbomb calorimeter. The analyses were confined to species that provided sufficient material in each of four seasonal samples.

Species diversity was calculated using Brillouin's measure of uncertainty (1962- quoted in Pielou, 1969) which treats the samples as finite populations to be studied for their own sake, rather than as representatives drawn from a large community. The formula used states that

$$H = \log \frac{N!}{N_1!\ N_2! \ldots N_s}$$

where H is the measure of diversity of a finite population

N is the total number of individuals in the population and

N_1, N_2 ....N_s are the number of individuals in species 1,2 ...s

The diversity 'H' is usually greatest in unpolluted waters and least in polluted waters.

The evenness of distribution of individuals among the species 'J', was calculated using

$$J = \frac{H}{\log s}$$

where s is the number of species.

RESULTS

Abundance and biomass Spatial and temporal changes in abundance and biomass of stony-bed invertebrates showed two main trends (Fig. 2 and Table 3). Spatially, there was a general downstream increase in both abundances and biomass, though values were always low at station 2 because of the blanketing effects of silt on the substratum. The highest values were for stations 7 and 8, where in summer some species proliferated rapidly in the warm polluted waters, and massive transient blooms of Hydra occurred (station 7 only).

Temporally, there were seasonal fluctuations in abundance and biomass, which differed from zone to zone but always included peaks in spring (September to November). In the Mountain Stream very few animals were present at the beginning of the study, until a slow-growing, insect-dominated community WMS (the winter mountain stream community - see Table 1) appeared in June. Abundance and biomass of its fauna were low through the winter, peaked in spring and then decreased as the winged adults emerged (January to March). Very small individuals of the new WMS community were already appearing in samples as the mature insects emerged, so levels of abundance and biomass remained higher than in the previous autumn (March to May 1975), when successive communities had not overlapped.

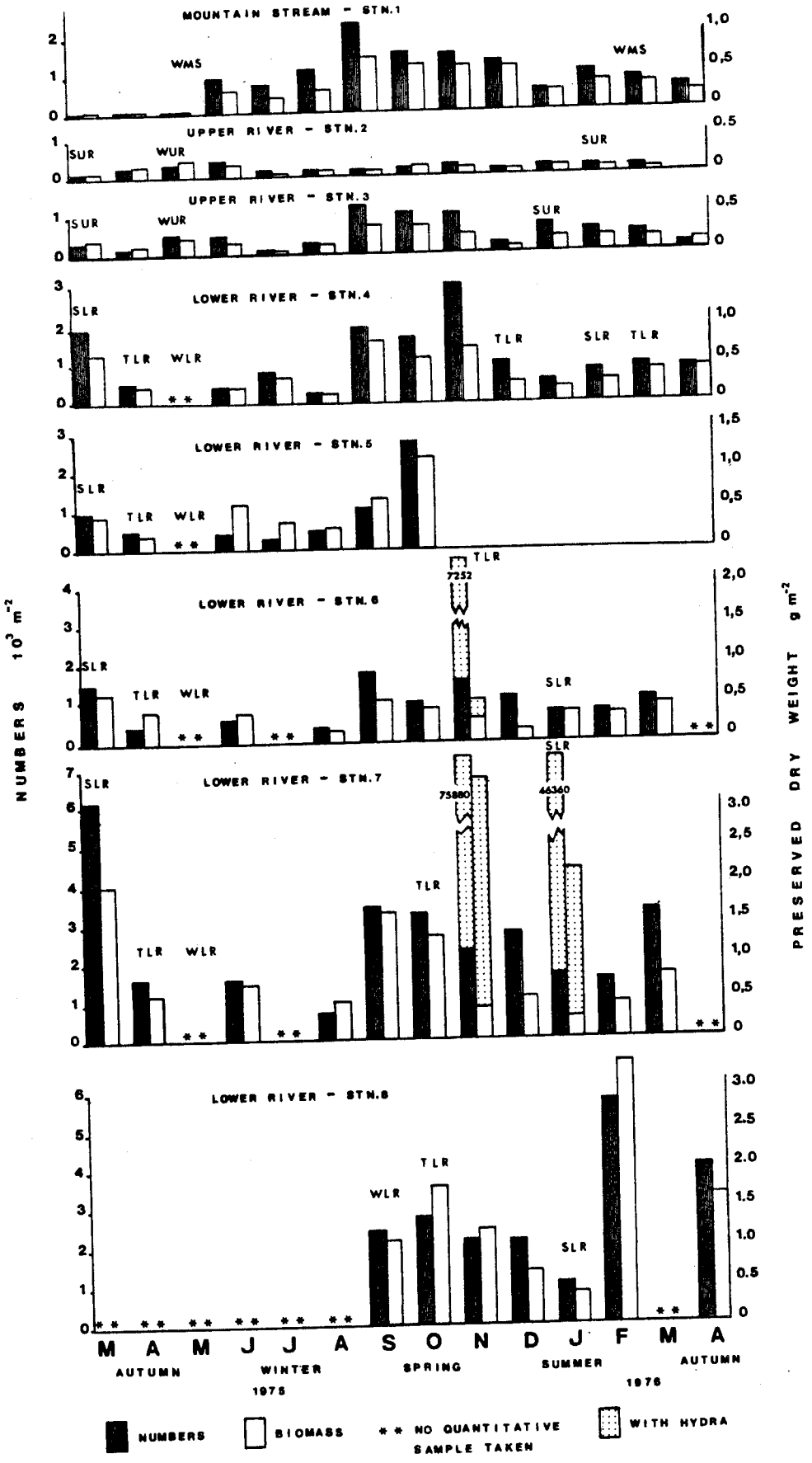

Fig. 2 Monthly abundance and biomass of the benthic macro-invertebrates at eight sampling stations along the Eerste River. Singly-occurring, large animals (Megaloptera, Odonata, Decapoda) have been excluded to avoid masking basic trends. The six faunal communities, WMS, WUR, WLR, SUR, TLR and SLR, are described briefly in the text and more fully in King (1981). The first appearance of a community at a station, and thus its replacement of the preceding community, is indicated for each station.

Table 3. Mean abundance and biomass (± S.E.) of stony-bed macroinvertebrates in three zones of the Eerste River, and in comparable zones of the Berg River (Harrison & Elsworth, 1958). Singly-occurring, large animals (Megaloptera, Odonata, Decapoda) are included in the figures. Values for Lower River (iii) of the Eerste River may be biased upwards, as they are based on samples taken in the drier months only.

Zone	Eerste River (sampler: 14 threads cm^{-1})			Berg River (sampler: 9 threads cm^{-1})	
	Station	Dry Weight g m^{-2}	Numbers m^{-2}	Numbers m^{-2}	Equivalent zone & station
Mountain Stream	1	0,447 ± 0,383	945 ± 640	1049	Mountain Torrent Station 1
Upper River	2	0,086 ± 0,056	209 ± 97	1281	Foothill, stony bottom 3/5
	3	0,284 ± 0,380	540 ± 324		
Lower River (i) (above sewage outfall)	4, 5, 6	0,620 ± 0,310	1200 ± 1210	1043	.. 9/10
Lower River (ii) (at sewage outfall)	7	1,529 ± 0,950 (1.167 without Hydra)	13325 ± 4580 (2580 without Hydra)	12186	.. 12
Lower River (iii) (below sewage outfall)	8	2,134 ± 1,880	3061 ± 1643	1151	.. 18

The turbid waters of the Upper River kept abundance and biomass levels at station 2 low throughout the year. While fluctuations were probably also somewhat suppressed at station 3, they could be related to the occurrence of the alternating winter and summer communities. An insect-dominated winter community WUR (the winter upper river community) appeared in May 1975, but abundance and biomass levels remained low through the winter. Values of both peaked in spring, then decreased again in December as the insects emerged and the community disappeared. The succeeding summer community SUR (the summer upper river community) was also dominated by insects. SUR had a high number of animals initially (January) and few animals finally (April), a pattern typical of insect-dominated streams, due to the emergence of winged adults (Hynes, 1970). Biomass remained much the same during most of the community's life-span, due to the increasing size of the decreasing number of animals. The tail-end of both SUR communities (March/April 1975 and April 1976) had high biomass levels in relation to numbers, indicating the presence of a few large animals just before the community disappeared.

The Lower River supported an alternating winter community WLR (the winter lower river community), with a high proportion of insects, and summer communities TLR and SLR (the transitional and summer lower river communities), with low proportions of insects. TLR, with a species composition intermediate between WLR and SLR, appeared in spring and autumn. It remained in the upper part of the zone through most of the summer (Fig. 2) but appeared only briefly further downstream, before giving way to the more pollution-tolerant SLR. In this study WLR appeared in May 1975, but abundance and biomass levels remained low through the winter, though relatively higher at station 7. Levels

of both peaked in spring as the winter animals matured, remained high as the transitional community TLR replaced WLR, then gradually fell until SLR replaced TLR (the trend is more obvious at station 7 if Hydra is excluded). With the appearance of SLR abundance and biomass levels rose rapidly, particularly at stations 7 and 8, and decreased again only in early autumn when rains returned some flow to the river (e.g. April 1975). TLR reappeared briefly at this time and was then replaced by the winter community WLR as the heavy rains began. With the onset of winter, abundance and biomass values fell to the low winter levels.

Full details of the contribution of each species to the abundance and biomass are given in Appendix I.

Calorific values Results of the calorific analyses are given in Appendix II. Values for the different species lay between 4,9, and 6,2 kcal g^{-1} dry weight of organic matter, with a mean of 5,6 kcal g^{-1} dry weight. Both the range and the mean lie within the limits given by Winberg (1971) for aquatic organisms. Seasonal differences were small except in the case of the mollusc Burnupia capensis; no explanation can be given for the very low summer value recorded for this species. Values for the inorganic fraction of the samples fell into four groups. Highest values were obtained for the Oligochaeta and the mollusc B. capensis (22,0 - 23,0%), and lowest values for the carnivores Chloroniella peringueyi, Aeschna minuscula and Pseudagrion salisburyense (2,6 - 3,4%). The Ephemeroptera formed an intermediate group, with values of 5,0 - 7,0%, while the three dipteran families fell within the limited range of 9,3 - 9,8%.

Species diversity Diversity of the Ephemeroptera has been calculated

Table 4. Mean species diversity 'H' and evenness 'J' of the Ephemeroptera at each sampling station, over the 14 months of the study.

Station	'H'	'J'
1	0,6339	0,6564
	D A M	
2	0,6992	0,6809
3	0,6264	0,6098
	STELLENBOSCH	
4	0,3755	0,4368
6	0,2694	0,3456
	SEWAGE-FARM OUTFALL	
7	0,1493	0,1843
8	0,1426	0,2872

as this group, represented by 20 species, occurred in every sample taken during the study and accounted for 32% of the total animal numbers (excluding Hydra). Some groups of animals, including the numerically-important Chironomidae, had not been identified to species level, so diversity of the fauna as a whole could not be calculated.

Mean species diversity 'H' and evenness 'J' of the Ephemeroptera over the study period decreased downstream (Table 4), except for small peaks at station 2 (below dam site) and an increase in 'J' at station 8. Values for both 'H' and 'J' decreased noticeably at Stellenbosch, and again at the sewage outfall. This was mainly due to the summer-time decline in both numbers and species in the Lower River. Ephemeroptera were abundant and diverse in nearby clean vleis (small lakes) and rivers during that summer (unpublished data), so the decline in their diversity in the lower reaches of the Eerste River could not be attributed to a general scarcity of the group.

Composition of the fauna The fauna was dominated by Ephemeroptera and Diptera (Fig. 3). The Ephemeroptera are an important component of the local riverine fauna, and were consistently well represented in samples from the Eerste River, except those taken from the Lower River during summer and autumn. The presence of Ephemeroptera tailed off sharply in this zone in early summer as flow decreased. Prominent ephemeropteran families were the Leptophlebiidae and Baetidae, with Castanophlebia calida and Baetis harrisoni the two most common species.

The high Diptera numbers were mainly due to the Blephariceridae in the Mountain Stream, Chironomidae in the Lower River, and a mixture of these two groups in the Upper River. Simuliidae were also

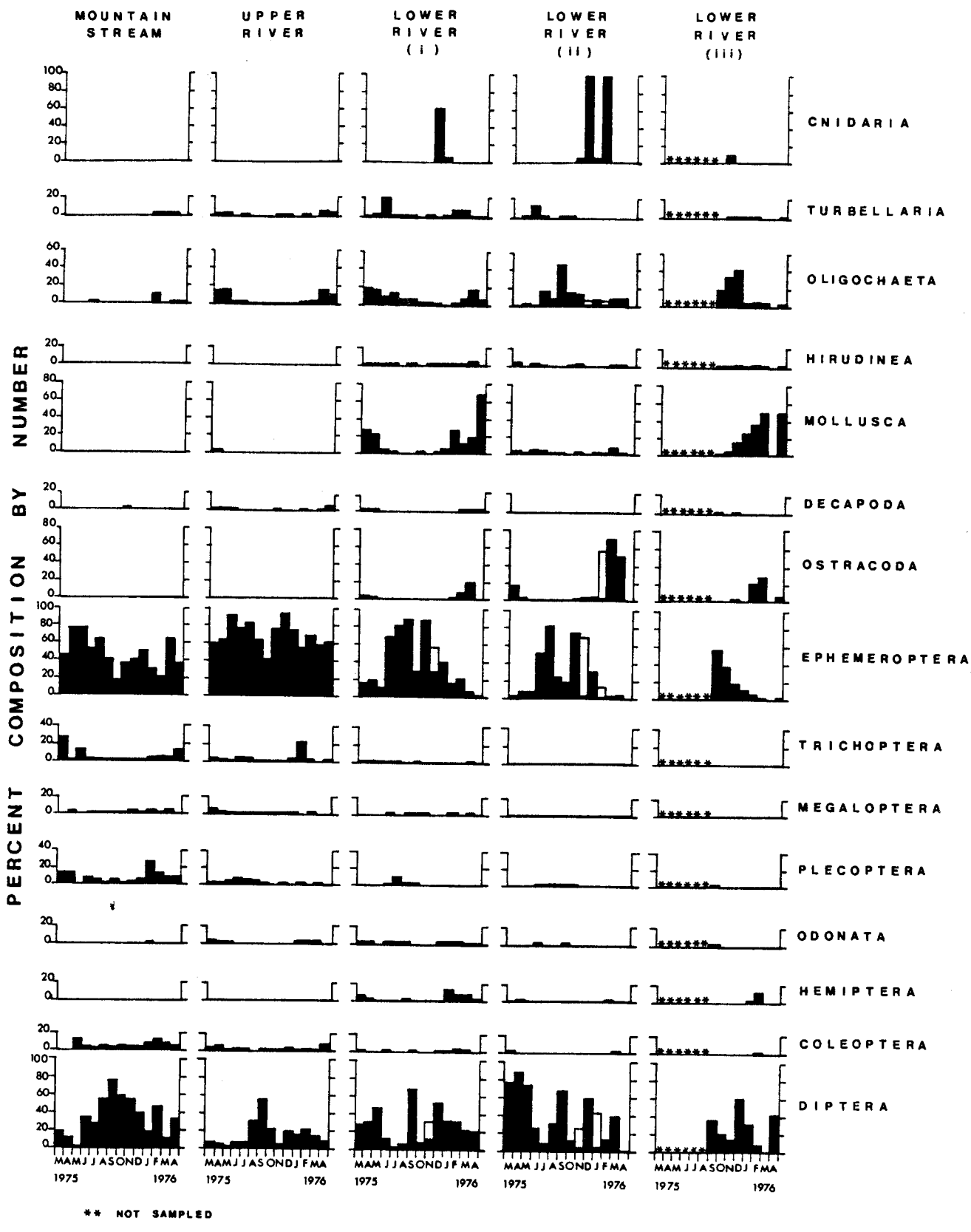

Fig. 3 Monthly percentage composition by number of the stony-bed fauna. Blank blocks indicate the composition of the fauna, if the blooms of *Hydra* are excluded.

occasionally abundant in the Mountain Stream and the Lower River. Blephariceridae in the Mountain Stream and Chironomidae in the Upper and Lower Rivers were responsible for the high numbers of Diptera throughout the river in September. While dipteran numbers were high in the Mountain Stream through the winter, decreasing after the September peak as the Blephariceridae emerged, they were generally highest in the Lower River in summer and autumn. The September peak there thus stood isolated among months of relatively low abundance (Fig. 3: Lower River (i)). The summer and autumn build-up of Diptera in the Lower River was due largely to Chironomus spp.

All other faunal groups either increased or decreased in abundance downstream (Fig. 3). The Trichoptera and Plecoptera, though always poorly represented, reached their highest numbers in late summer or autumn (January - April) in the Mountain Stream. Both groups were always present in this zone, but occurred mainly in winter in the Lower River. Two other groups, the Megaloptera and Coleoptera, were also most abundant in the Mountain Stream, being present though uncommon there throughout the year. While the Megaloptera did indeed decrease in numbers downstream, the data for the Coleoptera are misleading. Coleoptera were abundant in the Lower River, but were not of the rock-clinging families typical of mountain streams and so did not occur in stony-bed samples. Dytiscidae, Hydrophilidae and Gyrinidae, typical coleopteran families of the Lower River, were common in vegetation sweeps (King, 1981).

Most of the remaining groups - the Hirudinea, Ostracoda, Hemiptera, Mollusca, Oligochaeta, Turbellaria and Odonata - were most abundant in the Lower River, the first three groups being restricted to that zone (Fig. 3). Of these three, the Hirudinea were present throughout the

year and reached their highest numbers at the sewage outfall. The Ostracoda and Hemiptera occurred seasonally, in summer and autumn, with the Ostracoda abundant at the sewage outfall and the Hemiptera scarce there but common upstream and downstream. Molluscs were also largely confined to the Lower River, with only a few small and fragile individuals found in the Upper River. A few large animals maintained the winter presence of the group in the river, but numbers increased rapidly in summer. By early autumn the group accounted for 58% of the number of animals above the sewage outfall, 4% at the outfall and 47% below it. Molluscs became scarce at the beginning of winter, when flood waters scoured the river bed.

Trends in the Oligochaeta were less obvious than in other sections of the fauna, but the group was most abundant in the Lower River. The Decapoda, Turbellaria and Odonata were not sufficiently common for trends to become apparent. Hydra dominated the fauna at the sewage outfall (Lower River (ii)) in November and January. With Hydra excluded from the calculations, the composition of the remaining fauna was in agreement with adjacent months (Fig. 3), incorporating the beginning of the summer build-up of Ostracoda and Diptera and the decline of the Ephemeroptera.

DISCUSSION

Abundance, biomass and species diversity The validity of quantitative sampling in running waters has been discussed by, among others, Needham & Usinger (1956), Gaufin et al (1956), Chutter and Noble (1966), Schwoerbel (1970), Hynes (1970) and Bishop (1973). Sampling methods and the patchy distribution of the animals are recognised sources of

inaccuracy when estimating the abundance and biomass of stony-bed fauna, but a recently acknowledged phenomenon - that of vertical migration of the benthos down into the river bed - may also be important (Coleman & Hynes, 1970; Bishop, 1973; Hynes et al, 1976 and Hughes, 1978). Williams & Hynes (1974) showed that animals were most abundant at a depth of 10 cm in four Canadian rivers, while almost as many occurred at 70 cm depth as at the surface. In this survey, animals were collected to a depth of 10 cm, but what proportion of the total fauna this represents is not known. The spatial and temporal fluctuations in abundance, biomass, species diversity and species composition of this surface and immediately sub-surface portion of the fauna are, however, explicable, and are considered as representative of what was happening in the fauna as a whole (see below).

Downstream changes in abundance, biomass and species diversity of benthic invertebrates in the Eerste River (Fig. 2) can be related to changes in the physico-chemical quality of the water. Sharp drops in the levels of both abundance and biomass between stations 1 and 2, and their gradual increase again through stations 3 and 4, are a result of sediment entering the river above station 2. Diversity 'H' of the Ephemeroptera was higher at that station, however, than at any other (Table 4), despite the scarcity of animals. Small individuals of several different ephemeropteran species occurred sporadically and fleetingly on the river bed; none became established there. The Upper River forms could not cope with the sediment, and other factors (possibly low nutrient and mineral levels, high current speeds) precluded invasion by more sediment-tolerant Lower River forms. The response of the Ephemeroptera to the polluting sediment was mirrored by the fauna as a whole, and contrasted strongly with the response of a community to organic pollution, when a few species occur in very high numbers

(Hynes, 1974). High values of 'H' at station 2, similar to those in the Mountain Stream, falsely indicated an unpolluted environment. Other forms of 'alien' pollution (e.g. toxic chemicals), as opposed to the 'natural' pollution by an organic effluent, similarly could give misleadingly high values.

The high levels of abundance and biomass in the Lower River (Fig. 2) and the dissimilarity of its summer fauna to all other communities in the river, were the result of many factors, including water extraction, with subsequent poor summer flow, and high levels of organic pollutants. Sudden spring/summer blooms of Hydra indicated that the community of these nutrient-rich waters was unstable. The diversity 'H' of the Ephemeroptera declined downstream (Table 4), with major decreases at the town of Stellenbosch and at a sewage-farm outfall. The downstream decline in diversity can be correlated with the increasing levels of organic pollution along the river (King, 1981).

Seasonal changes in abundance and biomass were different in each zone and have been interpreted with reference to the communities occurring there. Very little is known of the life histories and biology of most South African freshwater invertebrates, however, and the following interpretations of the data may need to be modified in light of new knowledge. Each community produced simultaneous peaks in both abundance and biomass. There was one peak per year in the Mountain Stream, which supported a single (winter) community, and two peaks per year in the Upper and Lower Rivers, both of which supported winter and summer communities (Fig. 2). The winter communities of the three zones (WMS, WUR, WLR) had a similar species composition, and followed similar trends in animal numbers and biomass. Levels of both were

low in winter, peaked in spring, then declined until the winged adults had emerged and the communities disappeared. There was an upstream increase in the length of time a winter community lingered after the spring peak. The Lower River community, WLR, disappeared immediately after the peak, while the Upper River community, WUR, was present for a further 2-3 months, and the Mountain Stream community, WMS, for 3 - 4 months.

The summer communities of the Upper and Lower Rivers (SUR and TLR/SLR respectively) were quite dissimilar in species composition, and trends in their abundance and biomass levels were different. The Upper River community, SUR, was dominated by insects, and had high initial numbers and low final numbers. This suggests a largely univoltine fauna, with an initial mass appearance of juveniles and consequent loss of individuals through mortality and, later, through emergence of winged adults. The almost-constant level of biomass through all but the last days of the community's life, suggests continued growth of an ever-decreasing number of animals. The two summer communities of the Lower River, TLR and SLR, were not dominated by insects. As TLR replaced WLR, abundance and biomass levels remained at about the level of the spring peak, then gradually fell. The high values after the peak were due to a "fast" spring-time generation of Baetis harrisoni, and to an increase in the number of Oligochaeta. These animals, and the remnants of the winter fauna, declined in numbers in early summer as SLR replaced TLR. A fauna dominated by Mollusca, Chironomidae, Ostracoda and Oligochaeta then proliferated, causing abundance and biomass levels to rise rapidly through the summer and autumn. Values dropped slightly in late autumn as TLR reappeared, then fell to the low winter levels as the heavy rains began (see first three months of study period).

Unexplained fluctuations in abundance and biomass levels Samples collected from the river bed immediately after a spate contained very few animals, yet within a few days their numbers had risen to pre-spate levels again. The newly-appeared individuals were in the same size range as those that had disappeared, suggesting that animals had either retreated into the river bed during the spate and resurfaced later, or had been swept away and replaced from below. The phenomenon of vertical migration down into the river bed could account for the relatively low levels of abundance throughout the river in winter, and the sudden higher levels in spring (Fig. 2). Newly-hatched animals could not entirely account for the spring increase in numbers, as many of the animals found then were nearing maturity. Possibly only a portion of the fauna was at the surface of the substratum at any one time during winter, and the spring increases indicated a general upwards move of animals from deeper levels. Such a mass movement to the surface could be a response to the first slackening of current speeds at the end of the winter rains(i.e. in September, King, 1981) rather than a general preparation for the emergence of winged adults and the culmination of the communities. The winter communities of the two upper zones, for example, showed the September peaks in animal numbers and biomass, but did not disappear until some time later.

A general migration down into the river bed to avoid fast currents could account for the different fluctuations in abundance of the three insect-dominated winter communities (WMS, WUR, WLR) and of the one insect-dominated summer community (SUR). In the winter communities, numbers were generally low all winter, peaked in spring and then declined, while in the summer community the more characteristic pattern of high initial numbers and low final numbers was apparent. The low initial number of the winter communities could have been a result of

most of the animals being below the depth of the sampler, while the high initial numbers of the summer community suggest that the summer animals do not retreat into the river bed. Harrison & Elsworth (1958), when describing temporal changes in the abundance of stony-bed fauna of the nearby Berg River, mention an increase in numbers of individuals during a dry winter month, a decrease during subsequent wet months, and a later 'marked spring rise in numbers' at all stations.

Abundance and biomass of aquatic invertebrates - other rivers Comparison of the mean numbers of invertebrates in the Eerste and Berg Rivers (Table 3) shows that numbers remained much the same through the upper zones of the Berg, while falling in the Eerste due to the input of sediment from the dam site. The recovery of the numbers in Lower River (i) of the Eerste, to the same levels as in the Berg, suggests that influence of the sediment on the fauna was largely confined to the Upper River. Organic pollution produced similar large increases in animal numbers in both rivers (Lower River (ii)), though the increase in the Berg River was due to Simuliidae and Nais sp rather than to Hydra. At the last stretches of stony bed in the two rivers (Lower River (iii)), numbers were back to pre-pollution levels in the Berg, 130 km below the point of pollution, but remained high in the Eerste, 3 km below the point of pollution.

Comparison of animal biomass levels in rivers in general should be treated warily, due to the different sampling methods used, but there is a trend toward higher biomass levels in streams receiving a higher quality or quantity of edible, allochthonous detritus. The trend is largely confined to headwaters (Minshall, 1978; Vannote et al 1980), and even there other factors such as autochthonous primary production (Minshall, 1978) and the inorganic chemistry of the water, play a

Table 5. Mean abundance and biomass of stony-bed fauna: a comparison with results from other year-long studies of headwaters of relatively unpolluted streams.

Authors	River	Riverine vegetation	Sampler	Numbers m^{-2}	Dry weight g m^{-2}
Mackay & Kalff 1969	Canada	Deciduous	Hess.		
	West Creek		16 threads cm^{-1}	2130	1,90
Woodall & Wallace 1972	U.S.A.	1. Grass/Rhododendron	Surber.	1214	1,64 *
	Appalachian streams	2. Pine/Rhododendron	17 threads cm^{-1}	716	0,59 *
	N. Carolina	3. Rhododendron/mixed deciduous		804	1,07 *
		4. Deciduous		783	2,75 *
Egglishaw & McKay 1967	Scotland				
	1. Shelligan Burn	Deciduous	Kick sample.		
			12 meshes cm^{-1}	-	2,88
	2. River Almond	Treeless heather moor		-	0,93
	3. Allt dos Mhuicarain	"		-	0,70
King 1981	South Africa	Evergreen, heathlike	Square-framed sampler.		
	Eerste River	bush	14 meshes cm^{-1}	945	0,45

* Ash Free Dry Weight

largely undetermined role. Nevertheless, biomass levels in the Mountain Stream of the Eerste River were much lower than in a Canadian stream receiving deciduous leaves, in Appalachian streams receiving a 'prolific input of grass detritus', deciduous leaves or a mixture of deciduous and evergreen leaves, and in a Scottish burn with deciduous riverine vegetation (Table 5). Levels in the Eerste River were also slightly lower than in two Scottish rivers flowing through treeless heather moors and in an Appalachian stream receiving mainly pine needles and Rhododendron leaves (which are unpalatable to detritivores and/or resistant to decay - Woodall & Wallace, 1972). The very low levels in the Eerste River are probably partly due to the decay-resistant nature of the allochthonous detritus (unpublished data), and partly to the liability of the river to come down in spate, as such streams are known to have a less abundant and less varied fauna (Hynes, 1970).

Biomass levels do not necessarily indicate the levels of production in a stream. Nevertheless, in the headwaters of the Eerste River, low levels of animal biomass were associated with a low level of production. Although the Mountain Stream and Lower River (i) had similar mean annual biomass levels, the Mountain Stream supported only one year-long community per year, and thus produced less invertebrate biomass than did Lower River (i), which produced both a summer and winter community each year. Detailed data on the Ephemeroptera in the system reveal that univoltine species grew fastest and largest in the lower reaches, while bi- or multivoltine species produced more generations there than in the Mountain Stream.

Composition of the fauna Headwaters of perennial, montane streams of the south-western Cape support many cold-stenothermal, rheobiontic invertebrate species which appear to be the remains of an old palaeogenic and palaeoendemic (= Old Element) fauna with 'Gondwanaland' affinities (Stuckenberg, 1962; Harrison, 1965; Harrison, 1972). Mixed with these forms are cold-stenothermal, montane species of a Pan-Ethiopian (Sub-Saharan) fauna, many of which also exhibit regional endemicity. Lower reaches of the same rivers support more widespread, hardy species, also of Pan-Ethiopian origin.

The fauna of the Eerste River is typical of such streams, with both Old Element and Pan-Ethiopian forms present. Among those animals identified to generic or species level in this survey, and suggested by Harrison (1965) as representatives of the Old Element, are the ephemeropteran genera Aprionyx, Castanophlebia (both of which have affinities with South American and Australian forms - Barnard, 1932), Ephemerellina and Lestagella, the blephariceridsElporia spp., the megalopterans Chloroniella peringueyi and Platychauloides spp., the plecopterans Aphanicerca spp. and the coleopterans Peloriolus spp. and Epidelmis capensis. Other possible candidates are the trichopterans Barbarochthon and Petrothrincus.

Most of the species proposed by Harrison as being part of the Pan-Ethiopian fauna are in groups not identified to species level in this survey, so their presence in the Eerste River cannot be verified. He did, however, list three baetid mayflies Baetis harrisoni, Baetis bellus and Centroptilum sudafricanum, which occur in Southern Rhodesia (Zimbabwe) and southwards, and which occur in the Eerste River. Several other invertebrates typical of the lower reaches of the Eerste River

are widely distributed throughout the country, though they do not appear in Harrison's list of the Pan-Ethiopian fauna. Species of Corixidae, Pleidae, Dytiscidae, Caenidae, Aeschnaedae and other families, for instance, are common to both the Eerste River and the Jukskei-Crocodile system in the Transvaal (Allanson, 1960). In summer these species form part of the faunal communities in the lower reaches of the Eerste River, while the cold-stenothermal, rheobiontic species form the communities of the upper reaches. In winter the cold-stenothermal types tend to extend throughout the river, and most of the 'summer' species disappear from samples.

The Eerste River rises in the most southerly mainland mountains with permanent running water, and is separated from the isolated Table Mountain massif by the Cape Flats, an area of sand and sluggish, alkaline streams. It appears to be richer in species than the streams rising on Table Mountain (Harrison, 1972) but poorer than the nearby Berg River (Harrison & Elsworth, 1958; Coetzer, 1978) and other rivers of the western Cape (Harrison & Agnew, 1962).

CONCLUSIONS

Abundance and biomass of stony-bed macro-invertebrates of the Eerste River increased downstream, with the highest values recorded in the lowest part of the study area in summer. The trend could be correlated with increasing downstream enrichment of the river water by organic effluents, and with concentration of these effluents during the dry summer months.

Seasonal changes in abundance and biomass of macro-invertebrates differed along the length of the river, because of the presence of dissimilar animal communities. Levels were always low in winter, and peaked in spring. They then decreased again in the upper reaches in summer and autumn, while increasing rapidly in the lower reaches until the onset of the winter rains. It is suggested that the low winter values may have been partly due to vertical migration of the animals down into the river bed, to avoid fast currents. If such a phenomenon does occur, the figures given in this paper do not represent the standing crop of all benthic macroinvertebrates but of the unknown proportion of them which were in reach of the sampler.

Species diversity of the Ephemeroptera, which was felt to be representative of the diversity of the total macro-invertebrate fauna, decreased downstream. Major decreases in diversity could be correlated with major changes in the physico-chemical quality of the water: at a town and at a sewage-farm outfall. In the silt-laden waters below a dam construction-site, however, the fleeting occurrence of individuals of several different ephemeropteran species resulted in a high diversity index. Other forms of 'alien' pollution (e.g. toxic chemicals), as opposed to 'natural' organic pollution, similarly could result in high faunal diversity indices that falsely indicated unpolluted environments.

Composition of the fauna was typical of local rivers with mountain sources. Ephemeroptera and Diptera dominated the fauna, while several other groups characteristic of stony-bed habitats, e.g. Trichoptera and Plecoptera, were poorly represented. Many species of the upper reaches have a restricted distribution country-wide, while species of the lower reaches tend to occur more widely through southern Africa.

ACKNOWLEDGEMENTS

My sincere thanks to Drs G Branch, B Davies, J Day and R Siegfried for critically reviewing various drafts of the paper. The research was financed by the Council for Scientific and Industrial Resarch and the University of Cape Town. The SA Department of Forestry allowed me to work in the Jonkershoek Nature Reserve, which encompasses the Mountain Stream zone of the Eerste River.

Appendix 1. Seasonal changes in abundance (m^{-2}) and biomass (dry weight mg m^{-2}) of the fauna of the three zones. Values were obtained by combining all samples taken in the relevant zone and season, and adjusting the result to a total per m^2. Spring (Sp): September, October, November. Summer (Su): December, January, February. Autumn (A): March, April, May. Winter (W): June, July, August. Top line of numbers shows abundance, bottom line shows biomass. * Decapod biomass not ascertained.

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
CNIDARIA																			
Hydra	-	-	-	-	-	-	-	-	935,0	0,5	-	-	24514,	14904,0	-	-	36,7	-	-
	-	-	-	-	-	-	-	-	30,1	0,1	-	-	1006,7	640,9	-	-	3,3	-	-
TURBELLARIA	-	2,0	0,4	-	1,0	2,3	8,0	0,3	25,8	39,7	12,7	3,0	10,0	-	2,0	3,0	15,3	3,3	40,0
	-	1,0	0,3	-	0,5	1,2	2,5	0,1	9,9	15,3	4,8	1,0	3,5	-	2,4	1,8	7,5	1,6	20,0
OLIGOCHAETA	-	19,3	4,0	2,0	2,0	11,3	32,2	4,3	32,0	25,3	122,7	42,5	350,0	130,7	158,7	291,0	776,7	125,3	118,0
	-	4,9	0,6	0,3	14,0	16,9	22,0	15,1	116,4	10,4	87,0	101,7	438,7	76,7	82,5	472,5	745,7	104,5	96,4
HIRUDINEA																			
Glossiphonia	-	-	-	-	0,3	0,3	-	-	3,8	0,8	11,6	0,5	16,7	5,3	108,0	9,0	12,7	26,0	22,0
disjuncta	-	-	-	-	0,1	0,2	-	-	1,4	0,9	8,4	0,7	5,9	2,7	68,2	11,5	8,5	14,5	8,8
Batracobdella sp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,7	1,0	-	0,7	-
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0,5	0,2	-	0,3	-
Helobdella	-	-	-	-	-	-	-	-	-	0,3	1,0	-	-	-	0,7	-	-	-	-
conifera	-	-	-	-	-	-	-	-	-	0,2	1,2	-	-	-	0,5	-	-	-	-
Marsupiobdella	-	-	-	-	-	-	-	-	-	-	-	-	0,7	-	-	-	0,7	-	-
africana	-	-	-	-	-	-	-	-	-	-	-	-	0,3	-	-	-	1,5	-	-
MOLLUSCA																			
Physa sp	-	-	-	-	-	-	0,4	-	-	0,3	4,0	-	-	3,3	1,4	-	-	-	-
	-	-	-	-	-	-	0,2	-	-	0,2	1,5	-	-	8,8	4,0	-	-	-	-
Burnupia	-	-	-	-	-	0,3	-	-	15,0	115,7	230,2	3,0	3,3	64,0	52,0	38,0	153,3	1259,3	1974,0
capensis	-	-	-	-	-	0,1	-	-	7,0	64,6	102,2	2,8	2,0	58,5	45,7	28,5	129,6	624,9	1250,6
Lymnaea	-	-	-	-	-	-	-	0,3	-	-	4,9	-	-	-	-	-	-	-	-
columella	-	-	-	-	-	-	-	0,1	-	-	4,0	-	-	-	-	-	-	-	-
Bulinus	-	-	-	-	-	-	-	-	-	-	6,2	-	-	0,7	19,3	-	-	-	-
tropicus	-	-	-	-	-	-	-	-	-	-	26,7	-	-	7,5	123,2	-	-	-	-

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
DECAPODA																			
Potamon	0,7	-	-	-	0,3	0,3	2,4	-	-	1,0	2,7	-	-	-	0,7	-	1,3	-	-
perlatus	*	-	-	-	*	*	*	-	-	*	*	-	-	-	*	-	*	-	-
OSTRACODA (1 sp.)	-	-	-	-	-	-	-	-	-	23,3	43,8	-	9,3	661,3	860,7	-	1,3	604,0	180,0
	-	-	-	-	-	-	-	-	-	1,8	3,1	-	0,8	54,9	76,3	-	0,1	46,7	16,0
EPHEMEROPTERA																			
Aprionyx	-	1,3	10,0	-	-	1,0	0,2	-	-	-	-	-	-	-	-	-	-	-	-
peterseni	-	5,3	8,8	-	-	2,8	0,1	-	-	-	-	-	-	-	-	-	-	-	-
Aprionyx	32,0	58,7	41,6	10,7	0,3	1,0	-	5,0	-	-	-	0,3	-	-	-	1,0	-	-	-
rubicundus	19,7	61,1	18,3	12,5	0,4	0,9	-	4,7	-	-	-	0,1	-	-	-	0,7	-	-	-
Aprionyx	-	-	0,4	-	-	-	-	-	-	-	-	1,0	-	-	-	-	-	-	-
intermedius	-	-	0,4	-	-	-	-	-	-	-	-	0,5	-	-	-	-	-	-	-
Adenophlebia	-	-	2,8	-	-	0,6	30,7	0,6	0,4	-	0,3	8,0	0,7	-	-	4,0	-	-	-
peringueyella	-	-	4,5	-	-	0,3	43,0	1,8	4,1	-	0,2	22,8	4,0	-	-	13,2	-	-	-
Castanophlebia	165,3	63,3	30,4	164,0	91,7	2,3	21,8	94,7	78,7	-	-	63,8	60,7	-	-	45,0	13,3	-	-
calida	67,6	28,9	6,3	56,1	49,1	0,9	4,8	29,1	49,5	-	-	23,9	62,2	-	-	28,9	12,7	-	-
Choroterpes	-	6,0	0,4	1,3	0,3	0,3	-	4,3	-	-	-	-	-	-	-	-	-	-	-
elegans	-	2,3	0,1	0,3	0,3	0,1	-	0,7	-	-	-	-	-	-	-	-	-	-	-
Ephemerellina	10,7	2,0	-	8,7	3,0	-	-	2,7	3,7	-	-	-	-	-	-	-	-	-	-
barnardi	4,3	1,1	-	1,9	3,0	-	-	0,7	1,9	-	-	-	-	-	-	-	-	-	-
Ephemerellina	2,0	12,0	-	4,7	48,0	3,3	1,8	18,7	9,8	-	-	4,5	20,0	-	-	5,0	10,7	0,7	-
harrisoni	1,7	4,8	-	1,0	37,4	2,6	0,3	3,7	8,6	-	-	1,0	23,7	-	-	3,7	11,7	0,1	-
Lestagella	200,7	18,0	17,2	210,0	19,3	0,3	6,0	25,7	3,0	-	-	2,3	1,4	-	-	-	0,7	0,7	-
penicillata	84,7	7,4	2,3	50,4	10,8	0,3	1,2	6,3	1,5	-	-	0,3	0,5	-	-	-	0,4	0,1	-
Baetis bellus	-	-	-	-	-	38,7	2,7	-	0,6	-	0,8	0,3	-	-	0,7	1,0	-	0,7	-
	-	-	-	-	-	4,8	0,4	-	0,4	-	0,6	0,1	-	-	0,1	0,1	-	0,1	-
Baetis	86,0	114,0	31,2	32,0	242,0	94,0	70,7	35,0	967,0	152,7	28,4	209,0	1422,7	256,0	44,0	388,0	658,7	92,7	4,0
harrisoni	21,4	8,5	4,6	10,4	42,4	10,1	19,3	15,7	226,6	11,5	12,0	116,7	365,5	25,9	3,4	228,1	356,7	19,7	3,4
Baetis sp	-	-	-	-	-	-	0,4	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	0,2	-	-	-	-	-	-	-	-	-	-	-	-

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Acentrella	4,7	43,3	8,4	1,3	22,3	22,0	4,9	6,0	18,0	2,3	-	7,5	9,3	-	-	11,0	4,0	-	-
capensis	1,1	4,3	0,8	0,3	3,9	2,7	1,2	2,1	8,0	2,0	-	4,0	4,3	-	-	4,2	2,7	-	-
Centroptilum	-	-	2,0	-	0,7	6,3	9,6	2,3	1,0	-	-	10,8	-	-	-	2,0	0,7	-	-
sudafricanum	-	-	0,3	-	0,2	0,9	1,7	0,5	0,5	-	-	3,2	-	-	-	0,7	0,4	-	-
Centroptilum	-	-	-	-	-	1,3	2,0	-	-	21,3	4,8	-	-	-	1,4	-	-	-	-
excisum	-	-	-	-	-	0,3	0,5	-	-	9,0	2,0	-	-	-	1,0	-	-	-	-
Pseudocloeon	-	-	1,2	-	-	4,3	0,4	-	-	-	-	-	-	-	-	-	-	-	-
vinosum	-	-	0,3	-	-	0,7	0,2	-	-	-	-	-	-	-	-	-	-	-	-
Cloeon	-	-	-	-	-	-	-	-	-	7,3	2,3	-	-	1.4	-	-	-	3,3	-
lacunosum	-	-	-	-	-	-	-	-	-	5,1	1,7	-	-	1,0	-	-	-	2,2	-
Cloeon sp	-	-	-	-	-	1,6	-	-	-	-	2,3	-	-	-	-	-	-	-	-
	-	-	-	-	-	0,5	-	-	-	-	1,7	-	-	-	-	-	-	-	-
Afronurus	-	-	4,0	2,7	1,0	3,0	114,0	2,3	1,0	-	-	0,7	0,7	-	-	2,0	-	-	-
harrisoni	-	-	1,8	1,3	5,6	1,8	28,3	1,5	4,4	-	-	0,2	4,0	-	-	3,0	-	-	-
Austrocaenis sp	-	-	0,4	-	0,3	22,7	4,2	-	1,3	38,3	63,3	0,8	2,7	2,0	3,3	7,0	8,0	2,7	2,0
	-	-	0,1	-	0,1	6,7	2,3	-	0,6	21,6	34,0	0,1	1,3	0,7	1,9	1,7	2,9	1,3	0,6
TRICHOPTERA																			
Athripsodes	-	1,3	2,8	8,0	1,3	-	0,4	5,7	0,8	-	-	0,8	0,7	-	-	-	-	-	-
(bergensis group)	-	0,7	1,4	3,7	0,7	-	0,2	2,7	0,1	-	-	0,6	0,3	-	-	-	-	-	-
Athripsodes sp	-	0,7	16,4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	0,3	8,2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barbarochthon	-	-	1,2	-	-	-	-	-	-	-	-	0,5	-	-	-	-	-	-	-
brunneum	-	-	0,6	-	-	-	-	-	-	-	-	0,1	-	-	-	-	-	-	-
Agapetus sp	-	-	-	0,7	-	-	0,4	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	0,3	-	-	0,2	-	-	-	-	-	-	-	-	-	-	-	-
Petrothrincus	-	5,3	2,8	-	-	-	2,9	-	-	-	0,3	-	-	-	-	-	-	-	-
circularis	-	2,7	1,0	-	-	-	3,0	-	-	-	0,5	-	-	-	-	-	-	-	-
Cheumatopsyche	1,3	18,0	-	4,7	0,3	0,3	-	1,0	-	-	-	-	-	-	-	-	-	-	-
spp	1,3	18,0	-	7,2	0,3	0,3	-	1,0	-	-	-	-	-	-	-	-	-	-	-
Hydroptila	-	-	-	-	-	29,0	-	-	-	-	2,9	-	-	-	-	-	-	-	-
capensis	-	-	-	-	-	14,5	-	-	-	-	1,4	-	-	-	-	-	-	-	-

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Parecnomina	0,7	8,0	1,3	-	0,3	1,3	-	0,3	-	-	-	-	-	-	-	-	-	-	-
resima	0,7	4,7	0,5	-	0,3	0,8	-	0,5	-	-	-	-	-	-	-	-	-	-	-
MEGALOPTERA																			
Chloroniella	7,3	1,3	0,4	2,0	2,0	-	3,8	1,0	0,6	0,3	0,5	0,5	-	-	-	-	0,7	-	-
peringueyi	92,0	176,7	9,6	125,5	92,8	-	136,0	63,8	105,8	1,7	2,0	16,8	-	-	-	-	31,8	-	-
Platychauloides	5,3	5,3	1,2	0,7	-	0,6	0,2	-	-	-	-	-	-	-	-	-	-	-	-
sp	44,3	47,7	12,0	2,3	-	19,4	0,1	-	-	-	-	-	-	-	-	-	-	-	-
PLECOPTERA																			
Aphanicerca spp	40,7	97,3	22,4	29,3	4,7	0,3	5,1	16,0	4,0	-	-	11,0	3,3	-	-	9,0	2,0	-	-
	18,8	28,4	11,1	12,8	1,7	0,1	2,6	5,9	2,8	-	-	2,6	2,1	-	-	4,8	1,6	-	-
Aphanicercella	-	-	0,4	1,3	-	-	1,6	-	-	-	-	-	-	-	-	-	-	-	-
spp	-	-	0,1	0,3	-	-	0,9	-	-	-	-	-	-	-	-	-	-	-	-
ODONATA																			
Aeschna	-	0,7	-	-	-	0,7	2,4	-	-	0,3	2,9	1,5	0,7	-	-	10,0	2,0	-	-
minuscula	-	0,1	-	-	-	1,7	75,9	-	-	36,7	174,1	262,5	54,2	-	-	839,8	464,4	-	-
Crocothemis sp	-	-	-	-	-	-	-	-	-	1,3	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	1,7	-	-	-	-	-	-	-	-	-
Orthetrum sp	-	-	-	-	-	-	-	-	-	0,7	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	1,3	-	-	-	-	-	-	-	-	-
Pseudagrion	-	-	-	-	-	-	-	-	-	0,3	-	0,3	-	-	-	-	-	-	-
salisburyense	-	-	-	-	-	-	-	-	-	4,5	-	0,1	-	-	-	-	-	-	-
HEMIPTERA																			
Rhagovelia infern-	-	-	-	-	-	-	-	-	-	3,3	-	-	-	-	-	-	-	-	-
alis africana	-	-	-	-	-	-	-	-	-	1,0	-	-	-	-	-	-	-	-	-
Laccocoris sp	-	-	-	-	-	-	-	-	-	-	0,8	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-	5,3	-	-	-	-	-	-	-	-
Gerris																			
zuqualana	-	-	-	-	-	-	-	-	-	2,3	0,3	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	3,0	0,5	-	-	-	-	-	-	-	-

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Anisops varia	-	-	-	-	-	-	-	-	-	0,3	-	-	-	-	-	-	-	2,0	-
scutellata	-	-	-	-	-	-	-	-	-	1,0	-	-	-	-	-	-	-	1,8	-
Enithares	-	-	-	-	-	-	-	-	-	0,7	-	-	-	-	-	-	-	-	-
sobria	-	-	-	-	-	-	-	-	-	3,3	-	-	-	-	-	-	-	-	-
Enithares	-	-	-	-	-	-	-	-	-	1,7	-	-	-	-	-	-	-	-	-
chinai	-	-	-	-	-	-	-	-	-	8,4	-	-	-	-	-	-	-	-	-
Sigara	-	-	-	-	-	-	-	-	-	28,7	8,3	-	-	-	-	-	-	4,7	-
contortuplicata	-	-	-	-	-	-	-	-	-	22,0	4,0	-	-	-	-	-	-	6,5	-
Micronecta	-	-	-	-	-	-	-	-	-	10,0	16,4	-	-	3,3	0,7	-	-	224,7	-
scutellaris	-	-	-	-	-	-	-	-	-	1,7	6,5	-	-	2,5	0,3	-	-	95,8	-
COLEOPTERA																			
Hydrophilid	-	-	-	-	-	-	-	-	-	1,0	-	-	-	-	1,4	-	-	-	-
larvae	-	-	-	-	-	-	-	-	-	0,3	-	-	-	-	2,0	-	-	-	-
Herophydrus	-	-	-	-	-	-	-	-	-	-	0,8	-	-	-	-	-	-	-	-
oscillator	-	-	-	-	-	-	-	-	-	-	2,6	-	-	-	-	-	-	-	-
Dytiscid	-	-	-	-	-	-	-	-	-	6,0	5,1	-	-	0,7	24,7	-	-	2,0	2,0
larvae	-	-	-	-	-	-	-	-	-	2,6	2,7	-	-	0,4	17,8	-	-	0,9	1,2
Epidelmis cap-	12,0	8,7	-	0,7	1,3	2,0	-	-	0,8	0,7	-	-	-	-	-	-	-	-	-
ensis (adult)	2,9	8,4	-	0,1	0,1	0,6	-	-	0,3	0,3	-	-	-	-	-	-	-	-	-
Epidelmis cap-	12,0	4,7	16,0	13,3	0,7	1,3	1,8	0,7	-	-	-	-	-	-	-	-	-	-	-
ensis (larva)	3,5	1,1	4,4	3,4	0,1	0,2	0,4	0,3	-	-	-	-	-	-	-	-	-	-	-
Elmidae	-	8,0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(1 sp. adult)	-	7,7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Peloriolus sp	-	2,0	1,2	0,7	0,7	1,3	1,1	0,7	-	-	-	-	-	-	-	-	-	-	-
	-	0,6	0,2	0,2	0,1	0,3	0,5	0,3	-	-	-	-	-	-	-	-	-	-	-
Ptilodactylidae	2,0	6,7	4,8	2,0	1,3	2,7	1,8	0,3	-	-	-	-	-	-	-	-	-	-	-
(1 sp.)	1,6	4,5	4,3	2,5	0,3	1,4	2,7	0,4	-	-	-	-	-	-	-	-	-	-	-
Helodidae	2,0	10,0	-	1,3	-	0,7	1,1	1,3	-	-	-	-	-	-	-	-	-	-	-
Adult A	0,4	9,4	-	0,5	-	0,2	0,6	0,1	-	-	-	-	-	-	-	-	-	-	-

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Helodidae	-	3,3	-	3,3	-	-	0,9	0,7	-	-	-	0,3	-	-	-	-	-	-	-
Larva A	-	1,8	-	1,7	-	-	0,3	0,2	-	-	-	0,1	-	-	-	-	-	-	-
Helodidae	0,7	-	-	3,3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Larva B	0,1	-	-	1,1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Helodidae	-	12,0	0,8	-	-	0,3	-	-	-	-	-	-	-	-	-	-	-	-	-
Larva C	-	4,6	0,1	-	-	0,1	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydraenidae	3,3	4,7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(1 sp. adult)	1,5	4,7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryopidae	2,7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
(1 sp. adult)	1,3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DIPTERA																			
Chironomus spp	-	-	-	-	-	-	-	-	0,3	29,3	86,4	-	18,0	142,0	1715,3	83.0	2,0	76,0	24,0
	-	-	-	-	-	-	-	-	0,1	6,6	12,2	-	19,5	47,4	513,8	68.0	0,7	21,2	6,6
Other	42,0	8,7	4,4	2,0	156,3	39,0	6,2	4,0	553,0	40,0	120,0	25,8	988,7	191,3	602,7	209,0	250,7	198,7	250,0
Chironomidae	5,4	1,3	1,3	0,2	20,0	9,1	1,6	0,3	72,9	7,6	20,9	3,4	152,7	24,9	123,2	37,7	30,7	41,1	41,2
Simuliidae	130,7	187,3	35,2	78,0	3,3	22,0	4,4	2,0	79,3	234,0	17,3	-	88,7	468,0	136,7	1,0	123,3	433,3	1430,0
	41,5	40,5	6,0	17,1	0,3	3,3	0,7	0,3	23,7	45,8	5,7	-	25,5	98,9	37,4	0,2	39,6	91,2	217,8
Rhagionidae	6,7	0,3	13,2	10,0	4,0	1,3	3,3	3,3	2,3	-	-	2,5	4,0	-	-	6,0	0,7	-	-
	12,7	0,4	11,4	13,3	4,3	0,3	2,1	3,5	6,4	-	-	3,3	17,0	-	-	9,7	2,3	-	-
Culicidae	-	-	-	-	-	-	-	-	-	46,0	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	8,0	-	-	-	-	-	-	-	-	-
Blephariceridae	963,7	149,3	7,6	276,0	2,7	1,3	-	34,0	1,8	-	-	0,8	-	-	-	-	-	-	-
	259,1	60,1	0,6	39,8	1,1	0,1	-	10,4	1,5	-	-	0,3	-	-	-	-	-	-	-
Psychodidae	-	-	-	-	-	-	-	-	0,5	-	-	-	-	-	-	2,0	-	-	-
(1 sp. larva)	-	-	-	-	-	-	-	-	0,2	-	-	-	-	-	-	0,5	-	-	-
Tipulidae	-	-	-	-	-	0,7	-	0,7	-	-	-	-	-	-	-	-	-	-	-
(1 sp. larva)	-	-	-	-	-	3,3	-	0,7	-	-	-	-	-	-	-	-	-	-	-
Tipulidae	-	-	-	-	3,3	-	-	-	1,3	-	-	-	3,3	-	-	-	1,4	-	-
(1 sp. pupa)	-	-	-	-	1,5	-	-	-	1,1	-	-	-	1,9	-	-	-	0,7	-	-

SPECIES	MOUNTAIN STREAM				UPPER RIVER				LOWER RIVER (i)				LOWER RIVER (ii)				LOWER RIVER (iii)		
Season	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
Unidentified	-	-	-	-	2,0	-	-	-	2,0	-	0,2	0,8	2,0	-	-	1,0	-	-	-
larva - 1 sp.	-	-	-	-	0,4	-	-	-	1,2	-	0,4	0,4	2,5	-	-	0,4	-	-	-
Ephydridae	-	-	-	-	-	-	-	-	-	10,3	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	5,5	-	-	-	-	-	-	-	-	-

Appendix II Calorific values and percentage inorganic content of benthic macro-invertebrates of the Eerste River

Species	Calorific values by season (kJ g^{-1} dry weight)						kJ g^{-1} organic matter	kcal g^{-1} organic matter	% Inorganic *
	Autumn	Winter	Spring	Summer	Mean	SD			
OLIGOCHAETA	19,3	17,7	17,8	18,4	18,0	1,0	23,4	5,6	23,0
MOLLUSCA									
Burnupia capensis	18,9	-	-	13,4	16,2	3,9	20,7	4,9	22,0
EPHEMEROPTERA									
Castanophlebia calida	-	21,4	22,0	-	21,7	0,4	23,1	5,5	5,1
Ephemerellina harrisoni	-	23,5	23,7	-	23,6	0,1	24,8	5,9	5,0
Baetis harrisoni	23,7	21,8	22,5	23,3	22,8	0,9	24,2	5,8	5,6
Baetis bellus	18,9	23,8	20,1	21,7	21,1	2,1	22,7	5,4	7,0
MEGALOPTERA									
Chloroniella peringueyi	23,3	21,4	22,6	24,0	22,8	1,1	23,4	5,6	2,6
ODONATA									
Aeschna minuscula	21,0	21,4	22,8	21,5	21,7	0,8	22,5	5,4	3,4
Pseudagrion salisburyense	22,9	20,6	20,8	23,4	21,9	1,4	22,6	5,4	3,1
CHIRONOMIDAE	19,3	19,5	21,2	20,9	20,2	1,0	22,4	5,4	9,8
SIMULIIDAE	21,9	21,4	20,2	20,3	21,0	0,8	23,2	5,5	9,7
BLEPHARICERIDAE	-	23,6	23,6	-	23,6	0	26,0	6,2	9,3

* Inorganic remains after bomb calorimetry

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PART 3

SPECIES DISTRIBUTION, LIFE CYCLES AND EMERGENCE PHENOLOGY OF EPHEMEROPTERA IN THE EERSTE RIVER, CAPE PROVINCE, SOUTH AFRICA

SPECIES DISTRIBUTION, LIFE CYCLES AND EMERGENCE PHENOLOGY OF EPHEMEROPTERA IN THE EERSTE RIVER, CAPE PROVINCE, SOUTH AFRICA.

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ABSTRACT

The Eerste River rises 60 km east of Cape Town, in the Republic of South Africa. Samples of the macro-invertebrate fauna of the stony bed reaches, collected in 1975/76, indicated that the aquatic invertebrates were numerically dominated by Ephemeroptera and Diptera. The distribution, life cycles and emergence patterns of the 17 species of Ephemeroptera are presented here. Almost half of the species are endemic to acid headwaters of the region, appear to be quite specific in their environmental needs, and have univoltine life cycles. Most of the remaining species are more hardy, being widespread both within the river system and over the subcontinent, and have bi- or multivoltine life cycles. The influences of water temperature and food quality are discussed, and it is concluded that both are involved in producing the recorded differences in life-cycle patterns and growth rates down the river.

INTRODUCTION

Studies of the aquatic macro-invertebrates in South African rivers have been largely confined to records of their distribution and abundance, and of the relation of these to the physico-chemical quality of the water. Specific groups of commercial or medical importance have received more detailed attention, but for the majority of the fauna data on life histories, feeding habits, production or reproduction are unavailable.

Climates in South Africa range from sub-tropical in the north to warm temperate in the south, with rainfall in different areas occurring in summer (north and east), in winter (south-west), evenly throughout the year (south-east)or rarely (central and west). Such climatic differences must greatly influence the life cycles of riverine invertebrates, but as yet we do not know how. A more detailed understanding of the yearly pattern of events in rivers across the sub-continent would greatly boost our chances of identifying problem areas in them, and of producing wise management policies for them. As almost all South African rivers are interfered with, from dams on their headwaters to development of their estuaries, management based on a sound understanding of river ecology is of paramount importance.

The Ephemeroptera are numerically important in rivers throughout the country. A recent study of the species distribution and biomass of aquatic invertebrates in a small river in the south-western Cape Province, the Eerste River, revealed that Ephemeroptera and

Diptera dominated the fauna (King, in press). Species distribution, life cycles and emergence phenology of the Ephemeroptera in the Eerste River are described here, using data available from the original study. The data are incomplete, because of the generalised nature of the study, but nevertheless are sufficient to provide a basic picture of the dynamics of the group in the river. This is the first quantified information on life cycle patterns and growth rates of the Ephemeroptera of southern Africa.

STUDY AREA AND METHODS

The study area, methods and materials are described in King (1981). Briefly, the 40 km-long Eerste River rises in the Hottentots-Holland mountain range, 60 km east of Cape Town (Fig. 1). The upper 26 km stony section of the river comprised the study area. Discharge during the study ranged from a summer minimum, averaged over a month, of 0.33 m^3 sec^{-1}, to a winter maximum of 36.51 m^3 sec^{-1}. Water temperatures through the year were between 10°C and 28°C.

Three physical/biotic zones have been recognised down the length of the study area - the Mountain Stream, Upper River and Lower River zones (King, 1981). The gradients of the three zones are 24 m km^{-1}, 12 m km^{-1} and 2 m km^{-1} respectively. The catchment of the Mountain Stream supports indigenous, montane vegetation, while that of the two lower zones is given over to agricultural use. A town that discharges mainly organic effluents into the river is situated at the junction of the Upper and Lower River zones. Physico-chemical quality of the water below the town deteriorates each summer (December - February), due to water extraction and continued input of effluents, and improves each winter (June - August), due to increased flow. Quality of the water above the town is generally high, but sediment from a dam construction-site at the lower end of the Mountain Stream zone often covered the river bed of part of the Upper River during the course of this study (King, 1981; in press).

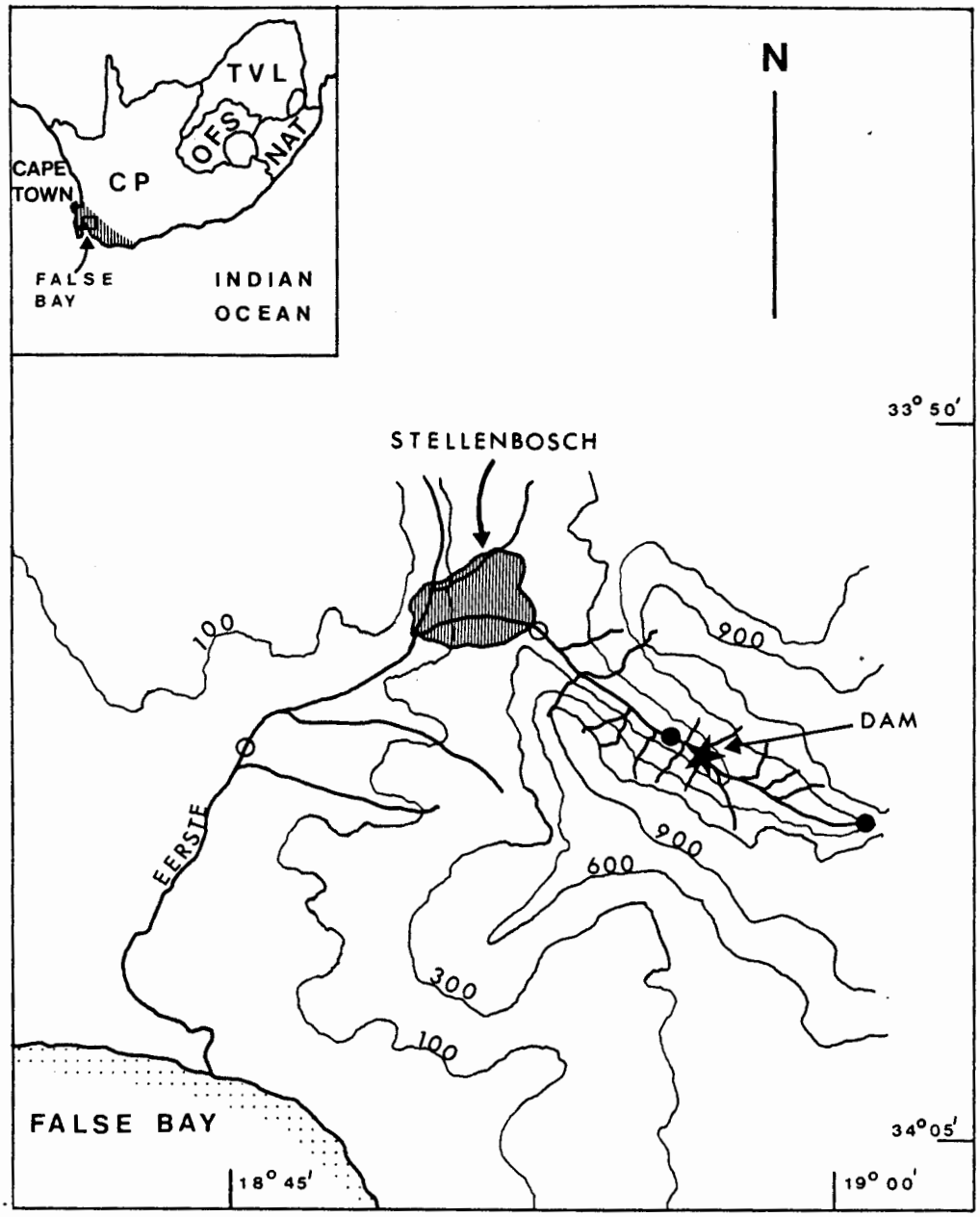


Fig. 1 Contour map of the Eerste River catchment, showing the study area (● to ● = Mountain Stream; ● to o = Upper River; o to o = Lower River), the town of Stellenbosch and the dam construction site. Contour lines in metres above sea level. Inset shows the location of the study area, the four provinces of South Africa (Cape Province, Orange Free State, Transvaal, Natal) and the winter rainfall area (hatched). Rainfall is increasingly non-seasonal north (little annual rainfall) and east (rain throughout the year) of this area, changing to a summer rainfall in the Transvaal and Natal.

Monthly samples of the macro-invertebrates were collected along the river between March 1975 and April 1976. Samples were taken from 0.5 m^2 of stony bed, and from 1 m^3 of marginal vegetation, and were preserved in 5% formaldehyde. All netting used was of 0.6 mm mesh, which collected animals as small as 1 mm length. Ephemeropteran nymphs in the samples were identified to species, counted and measured for body length using a dissecting microscope with an ocular micrometer. The major divisions on the micrometer, 0.8 mm apart, were used as size classes.

Presence of black wing-pads, which occur on the short-lived final nymphal instar, have been used to indicate when the flight periods of the adults were likely to have begun.

RESULTS

The Ephemeroptera accounted for 32% of the total number of macro-invertebrates collected from the stony bed, and 10% of those collected from the marginal vegetation (King, in press). Throughout the year the stony bed was available to the animals, and was always well-populated (Fig. 2). The marginal vegetation, on the other hand, was a more variable and seemingly harsher environment (King, 1981). Tough leaves of palmiet *Prionium serratum*, virtually the only submerged vegetation in the Mountain Stream and Upper River, provided a sparse refuge for small animals, and in summer were left dry by receding water levels. Animals were thus rare in the marginal vegetation of the two upper zones though plentiful in the submerged grasses and trailing *Tradescantia* of the lower zone. Generally, the total abundance of Ephemeroptera in each habitat increased downstream, and was highest in winter and spring (Fig. 2).

Seventeen species of Ephemeroptera were collected regularly, with the Leptophlebiidae and Baetidae being the most prominent families. Distinct spatial and temporal distributions of species were recorded (Fig. 2). The longitudinal distribution and abundance of species were different in each of the three zones, because of downstream changes in water quality. Seasonally, most species were characteristically found in either the wet winter and spring months or the dry summer and autumn months. In this paper such species have been called winter and summer species respectively. The

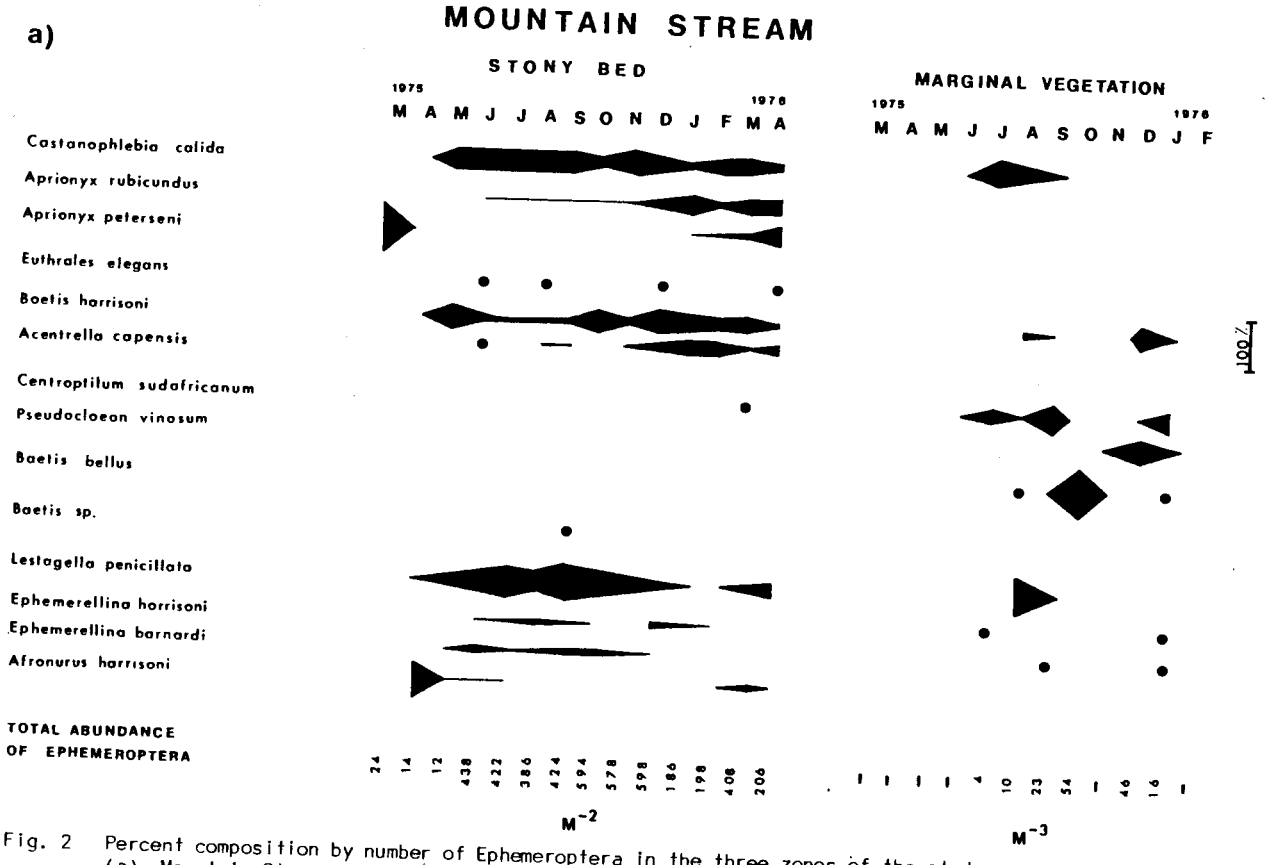
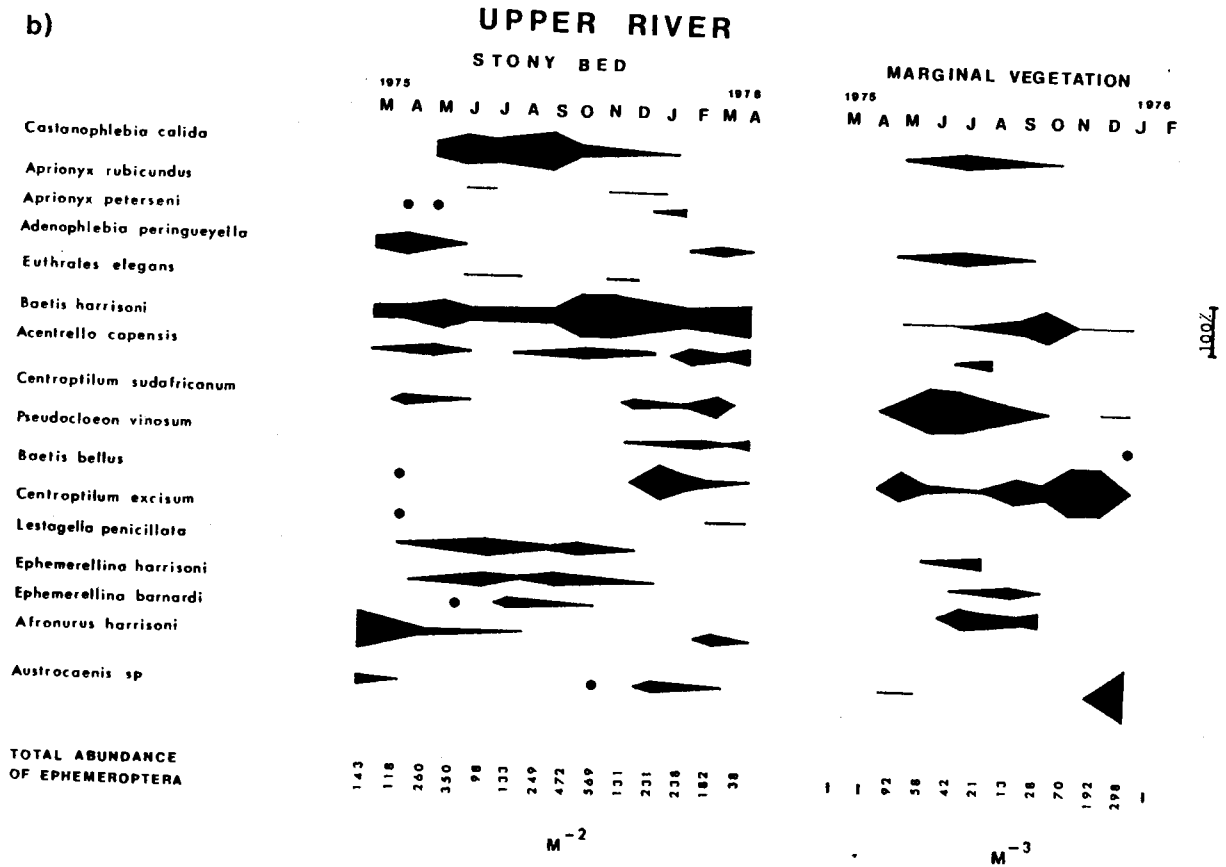
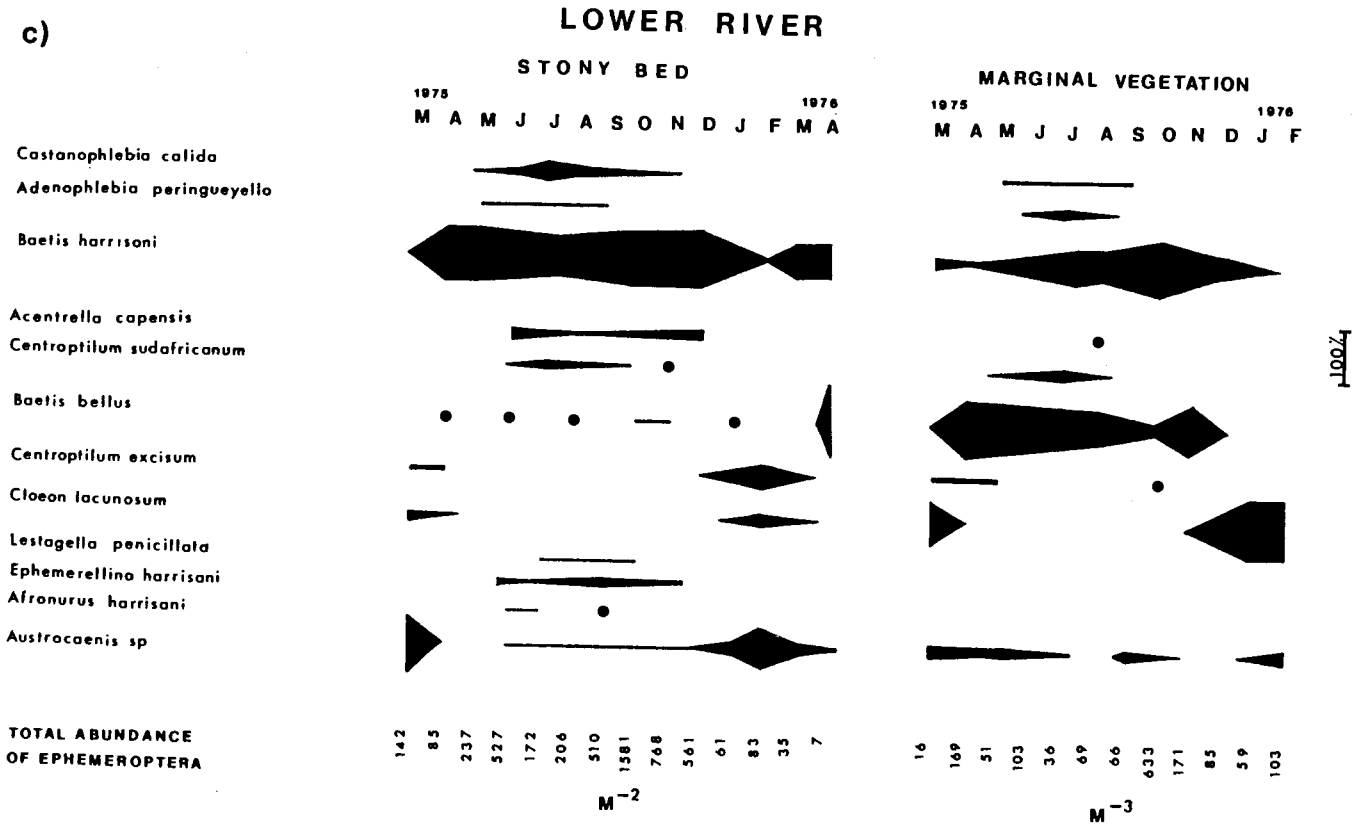


Fig. 2 Percent composition by number of Ephemeroptera in the three zones of the study area: (a) Mountain Stream; (b) Upper River; (c) Lower River. Total abundance of ephemeropterans per m^2 of stony bed and per m^3 of marginal vegetation, is shown for each zone.

b)


UPPER RIVER
STONY BED
MARGINAL VEGETATION
1975
1976
M A M J J A S O N D J F M A
M A M J J A S O N D J F
Castanophlebia calida
Aprionyx rubicundus
Aprionyx peterseni
Adenophlebia peringueyella
Euthrates elegans
Baetis harrisoni
Acentrella capensis
Centroptilum sudafricanum
Pseudocloeon vinosum
Baetis bellus
Centroptilum excisum
Lestagella penicillata
Ephemerellina harrisoni
Ephemerellina barnardi
Afronurus harrisoni
Austrocaenis sp
100%
TOTAL ABUNDANCE OF EPHEMEROPTERA
143 118 260 350 98 133 249 472 569 131 231 238 182 38
1 1 92 58 42 21 13 26 70 192 298 1
M-2
M-3


c)
LOWER RIVER
STONY BED
MARGINAL VEGETATION
1975
1976
M A M J J A S O N D J F M A
M A M J J A S O N D J F
Castanophlebia calida
Adenophlebia peringueyella
Baetis harrisoni
Acentrella capensis
Centroptilum sudafricanum
Baetis bellus
Centroptilum excisum
Cloeon lacunosum
Lestagella penicillata
Ephemerellina harrisani
Afronurus harrisani
Austrocaenis sp
100%
TOTAL ABUNDANCE OF EPHEMEROPTERA
142 85 237 527 172 206 510 1381 768 561 61 83 35 7
M-2
16 169 51 103 36 69 66 633 171 85 59 103
M-3

seasonality of occurrence was most obvious in the Lower River, where the annual ranges in flow, water temperature and chemical quality of the water were greatest (Fig. 2c). Seasonal changes in species composition were least obvious in the stony-bed habitat of the Mountain Stream, where some winter species lingered on through the summer (Fig. 2a).

Species distribution

Distribution of the 17 species of Ephemeroptera among families was: Leptophlebiidae 5; Baetidae 7; Ephemerellidae 3; Heptageniidae 1; Caenidae 1. The Leptophlebiidae were characteristically found on the stony bed. The most common species, *Castanophlebia calida*, appeared in all three zones when the winter rains began in May (Fig. 2). Though occurring in the Lower River only during the six wettest months, its presence was protracted upstream, and extended through most of the year in the Mountain Stream. *Aprionyx rubicundus* and *Choroterpes elegans*, present but uncommon in the Mountain Stream, tentatively have been placed with *C. calida* as winter species. They were present as nymphs at the same time, and most records of their imagos cover the same flight period (Barnard, 1932). In contrast, *Aprionyx peterseni* and *Adenophlebia peringueyella*, characteristic of the Mountain Stream and Upper River respectively, were collected mainly in autumn. Neither species was common.

The Baetidae were abundant in all three zones, with the number of species and individuals generally increasing downstream. The

family included two species characteristic of the stony-bed habitat (*Acentrella capensis* and *Centroptilum excisum*), four species characteristically found in marginal vegetation (*Centroptilum sudafricanum*, *Baetis bellus*, *Pseudocloeon vinosum* and *Cloeon lacunosum*), and the ubiquitous *Baetis harrisoni* which was abundant in both habitats. *B. harrisoni* was common in all three zones through most of the year, being rare only in the Lower River in late summer and autumn (Fig. 2). *Acentrella capensis* though never common, was similarly distributed. The reduced abundance of these two species in the Lower River during the dry season was part of a sharp decline in numbers of all Ephemeroptera there, which could be correlated with deterioration of the physico-chemical quality of the water (King, 1981). In early summer, however, the number of baetid species in the Lower River was at its highest. The increase was partly due to the appearance of *Cloeon lacunosum* in the slow-flowing waters - this species is present in neighbouring lentic waters throughout the year. *Centroptilum excisum*, a species of still backwaters in rocky streams, also appeared in the Lower River at this time but, like *C. lacunosum*, disappeared in late summer where water quality was poorest. Both *C. excisum* and *C. lacunosum* were absent during the winter months of high discharge. *Baetis bellus*, and to a lesser extent *Centroptilum sudafricanum*, occurred in marginal vegetation in the Upper and Lower River zones through most of the year. In the Upper River in autumn, when receding water levels left the vegetation dry, they were forced down onto the stony bed (Fig. 2b). *Pseudocloeon vinosum*, present but scarce in the marginal vegetation of the two upper zones, similarly appeared on the stony bed at this time.

The three ephemerellid species occurred on the stony bed in all three zones, though their numbers decreased downstream (Fig. 2). All were characteristic winter species, and were absent from samples taken during the hottest months. The two species sufficiently abundant for trends to be seen - *Lestagella penicillata* (Mountain Stream) and *Ephemerellina harrisoni* (Upper River) - showed a similar pattern of occurrence to the leptophlebiid *Castanophlebia calida*, appearing in samples at the beginning of winter, and later disappearing first from the Lower River and progressively later from upstream sites. Both were briefly absent from the Mountain Stream during summer and autumn 1976, unlike *C. calida*, whose nymphs were continually found.

The heptageniid *Afronurus harrisoni* (Upper River), and the caenid *Austrocaenis* sp. (Lower River) were summer species. Both were important components of the Ephemeroptera on the stony bed, during the limited late summer and early autumn period of minimal discharge, and both were collected occasionally during winter.

Life cycles

Interpretation of the variety of life cycles exhibited by the Ephemeroptera is complicated by the small numbers of some species found. Additionally, data are not available on the presence of eggs and very small nymphs on the river bed, nor on the occurrence of imagos. Using the available information, the 17 species have been

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placed in three groups, according to their time of main occurrence as nymphs in the Eerste River (Table 1). The placement of some rare species is tentative pending more information, and the groups themselves are not necessarily representative of different kinds of life cycles, but are merely a convenient way of condensing the data.

A winter group of seven species occurred principally during winter and spring, while a summer group of six species was typically found in summer and autumn (Table 1). A third hardy group of four species maintained a common or sporadic presence through most of the study area and through most of the year. Species that were present year-round in the Mountain Stream only were not included in the group, as the zone is known to support a year-long community (King, 1981). The two lower zones, on the other hand, have clearly defined summer and winter communities. Animals that superseded these boundaries and occurred there throughout the year, have been placed in the hardy group. Life cycles of representative species for each group are described below. Further details on the changes in mean length of the nymphs of all species during the year, and the time at which final-instar nymphs appeared, are given in Table 2.

a) The winter group: This group consists of three leptophlebiid species (*Castanophlebia calida, Aprionyx rubicundus, Choroterpes elegans*), three ephemerellid species (*Lestagella penicillata, Ephemerellina harrisoni, Ephemerellina barnardi*) and possibly one baetid species (*Pseudocloeon vinosum*). All but *P. vinosum* are typically found on the stony bed. Nymphs of the seven species

TABLE 1 Summary of the time of occurrence and the principal habitat of the 17 species of Ephemeroptera in the Eerste River

	Stony bed	Marginal vegetation
The winter group	*Castanophlebia calida* Barnard	*Pseudocloeon vinosum* Barnard
	Aprionyx rubicundus Barnard	
	Choroterpes elegans (Barnard)	
	Lestagella penicillata (Barnard)	
	Ephemerellina harrisoni (Barnard)	
	Ephemerellina barnardi Lestage	
The summer group	*Adenophlebia peringueyella* Lestage	*Cloeon lacunosum* Barnard
	Aprionyx peterseni (Lestage)	
	Afronurus harrisoni Barnard	
	Centroptilum excisum Barnard	
	Austrocaenis sp.	
The hardy group (year-round)	*Baetis harrisoni* Barnard	*Baetis bellus* Barnard
	Acentrella capensis Barnard	*Centroptilum sudafricanum* Lestage

TABLE 2 Monthly changes in mean lengths (mm) of Ephemeroptera in the Eerste River. River zones: M.S. = Mountain Stream; U.R. = Upper River; L.R. = Lower River; ns = no sample taken; * = sample includes final-instar nymphs with black wing-buds.

	River Zone	1975 M	A	M	J	J	A	S	O	N	D	1976 J	F	M	A
a) The winter group															
Cistanophlebia calida	M.S.	-	-	4.40	4.52	4.53	4.87	4.60	4.84	5.11*	4.71*	4.88	5.32	3.04	3.71
	U.R.	-	-	3.30	4.03	4.69	4.79	5.49*	5.20*	5.85	4.67*	3.60	-	-	-
++	L.R.	-	-	-	4.77	5.11	6.29	6.59*	6.19*	6.00	-	-	-	-	-
Aprionyx rubicundus	M.S.	-	-	-	5.90	6.40	8.60	5.20	5.50	5.20	6.10	6.10	6.30	4.70	5.50
++	U.R.	-	-	-	6.50	6.80	-	-	-	6.80	5.60	7.60	-	-	-
Choroterpes elegans	M.S.	-	-	-	3.60	-	3.60	-	-	-	4.62	-	-	-	1.20
++	U.R.	-	-	-	3.60	3.20	3.60	-	-	5.20	5.20*	-	-	-	-
Lestagella penicillata	M.S.	-	2.00	2.80	3.05	3.11	3.70	2.98	4.43	4.59*	4.43*	-	-	1.64	2.38
	U.R.	-	2.00	2.38	2.95	3.38	3.37	4.67	4.79*	4.82*	6.00*	-	-	-	-
++	L.R.	-	-	-	-	3.20	3.60	5.20	4.80*	-	-	-	-	-	-
Ephemerellina harrisoni	M.S.	-	-	-	2.00	2.00	3.33	3.60	4.60	-	3.00	4.40	6.80	-	-
	U.R.	-	-	1.77	2.41	2.45	3.07	4.80	5.36*	4.48*	4.06*	6.00	-	-	-
++	L.R.	-	-	-	2.96	3.60	3.94	5.66	6.27*	6.00*	-	-	-	-	-
Ephemerellina barnardi	M.S.	-	-	-	2.72	2.00	2.80	4.80	4.56	5.07	5.78	-	-	-	-
++	U.R.	-	-	-	2.00	-	3.73	4.74	4.40	6.80	-	-	-	-	-
Pseudocloeon vinosum	M.S.	-	-	-	-	-	-	-	-	-	6.00	4.80	-	ns	ns
++	U.R.	-	-	-	-	-	-	-	-	-	4.40	3.30	-	ns	ns
b) The summer group															
Aprionyx peterseni	M.S.	9.60	-	-	-	-	-	-	-	-	-	10.80	12.40	7.07	4.72
++	U.R.	-	3.60	-	-	-	-	-	-	-	-	10.80	5.68	-	-
Adenophlebia peringueyella	U.R.	5.98	6.25	7.89	9.20	-	-	-	-	-	-	-	4.40	3.92	5.20
++	L.R.	-	6.80	-	8.97	10.96	12.40	13.00	-	-	-	-	-	-	-
Afronurus harrisoni	M.S.	-	4.60	-	2.80	4.80	-	-	-	-	-	-	-	3.44	2.80
	U.R.	4.43	5.45	3.81	3.40	4.93	-	-	8.40	10.40	-	2.00	-	4.20	5.04
++	L.R.	-	-	-	4.13	3.60	-	10.00	6.80	-	-	-	-	-	-
Centroptilum excisum	U.R.	-	4.93	-	-	-	-	-	-	-	-	3.80	-	4.40	2.00
	L.R.	5.87	5.87	-	-	-	-	-	-	-	5.20	4.51*	5.32*	5.20*	-
Cloeon lacunosum	L.R.	5.75	6.44	-	4.44	-	-	-	-	-	5.54	6.10	5.72*	ns	ns
Austrocaenis sp.	U.R.	4.40	2.80	-	-	-	-	-	-	3.60	-	3.56	3.77	5.07	-
	L.R.	5.11	3.60	-	3.70	-	2.80	4.00	3.94	5.07	3.20	4.40	4.73	4.53	3.60
c) The hardy group															
Baetis harrisoni	M.S.	-	-	4.67	4.34	4.67	4.76	3.72*	4.22*	4.17*	2.78	2.78	2.61	2.94	3.92
	U.R.	4.36*	3.82	4.15	4.76	4.49	5.46	6.02*	3.69*	2.85*	2.27	2.78	3.33*	3.53*	3.50
	L.R.	5.20	4.92	4.56	5.58*	5.42*	5.71*	6.49*	3.52*	3.24*	3.10*	3.65*	-	4.62	6.27
Baetis bellus	M.S.	-	-	-	-	-	3.60	-	5.20	-	-	5.20*	-	ns	ns
	U.R.	-	-	4.47	6.00	-	4.40	6.18	5.20*	4.79	4.58	4.93*	-	ns	ns
	L.R.	-	4.63	5.08	5.09	5.20	5.92*	6.07*	5.72*	5.24*	5.25*	-	-	ns	ns
Centroptilum sudafricanum	M.S.	-	-	-	-	5.20	-	3.87	-	-	-	4.06	-	ns	ns
	U.R.	-	-	4.00	3.93	4.12*	4.54	5.20	5.20	-	4.40*	4.80*	-	ns	ns
	L.R.	-	-	4.00	4.64	5.36*	5.34*	5.55*	-	-	-	-	-	ns	ns
Acentrella capensis	M.S.	-	-	-	4.40	-	2.00	4.40	-	4.40	2.74	2.40	2.75	3.20	2.63
	U.R.	3.33	3.20	2.80	3.67	-	5.73	4.40	3.60	3.16	3.40	-	2.67	3.96	3.87*
	L.R.	-	-	-	4.40	5.33	5.47	5.53*	4.66*	3.40	3.26	-	-	-	-

++ = species thought to have univoltine life cycles, to be acid-water species and to be endemic to the region or some combination of these three.

occurred mainly in winter and spring, and were most abundant in one of the two higher zones, with numbers tailing off downstream. When water temperatures increased and discharge fell in spring, they disappeared first from the Lower River and progressively later from the Upper River and Mountain Stream. *Castanophlebia calida* exhibited a typical life cycle. Small nymphs of *C. calida* appeared throughout the study area as the winter rains began in May (Fig. 3a) and grew slowly through the winter. Emergence of imagos began in the Upper and Lower River zones in September and in the Mountain Stream in November. The species disappeared first from the Lower River and later from the Upper River but remained continuously present in the Mountain Stream. This was because a new generation of small nymphs appeared there in March 1976, overlapping with late-maturing nymphs of the previous generation. *Aprionyx rubicundus* also showed this overlap of generations in the Mountain Stream, while four of the remaining five species disappeared from samples for 2 - 4 months in the summer and autumn. The fifth species *Pseudocloeon vinosum*, was absent for all but two summer months, when large nymphs were found.

Changes in mean length of *Castanophlebia calida* through the months suggest it is univoltine (Fig. 3a). In each zone, mean length of the nymphs was small at the beginning of winter, increased until final-instar nymphs began to appear, and then dropped. The species then disappeared from the Upper and Lower Rivers, while the mean length of the continuously present

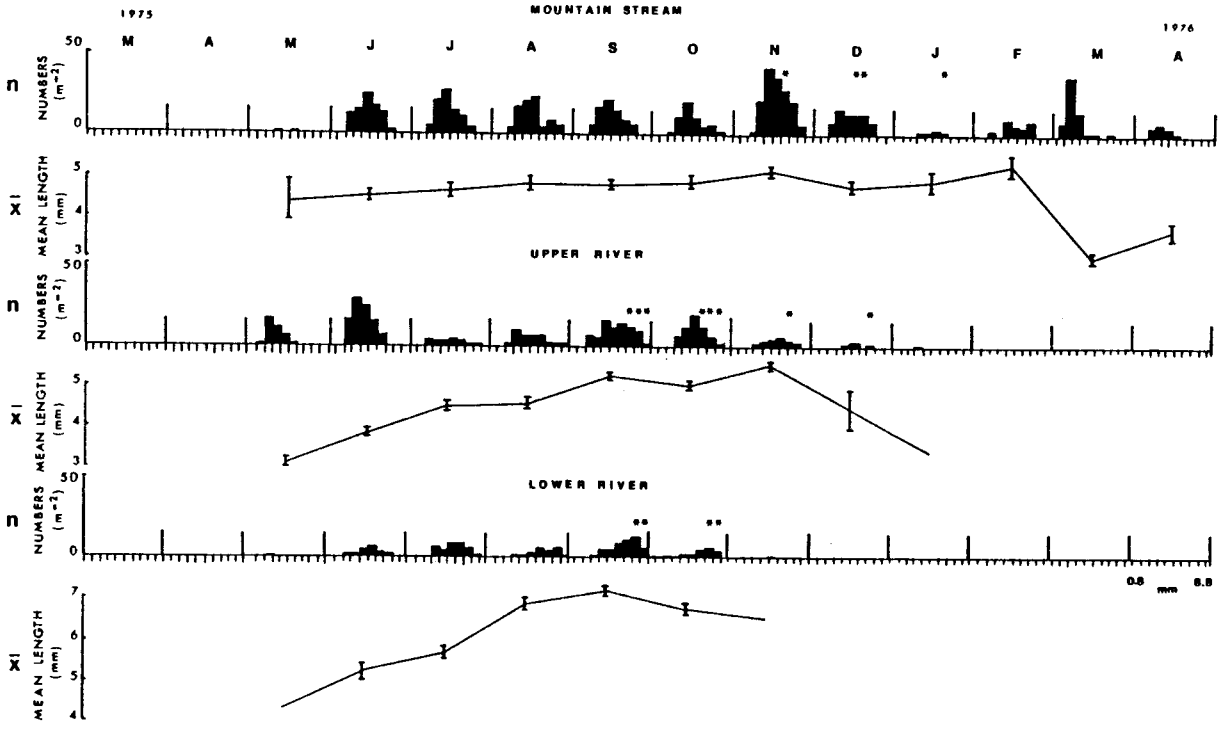

Fig. 3 Differing patterns of occurrence and growth of representative species of Ephemeroptera, in three zones of the Eerste River. Histograms show the size distribution of nymphs using the scale of body length given at bottom right. The accompanying graphs show changes in mean length (± S.E.) of the nymphs, and thus the different growth rates in each zone. * = Final-instar nymphs.

3a) *Castanophlebia calida*. A winter species with a univoltine life cycle. Growth is slowest in the Mountain Stream, where the life cycle lasts one year and the new generation appearing in autumn may overlap with the maturing one.. Nymphs grow faster and larger downstream, and emerge earlier - mainly in spring.

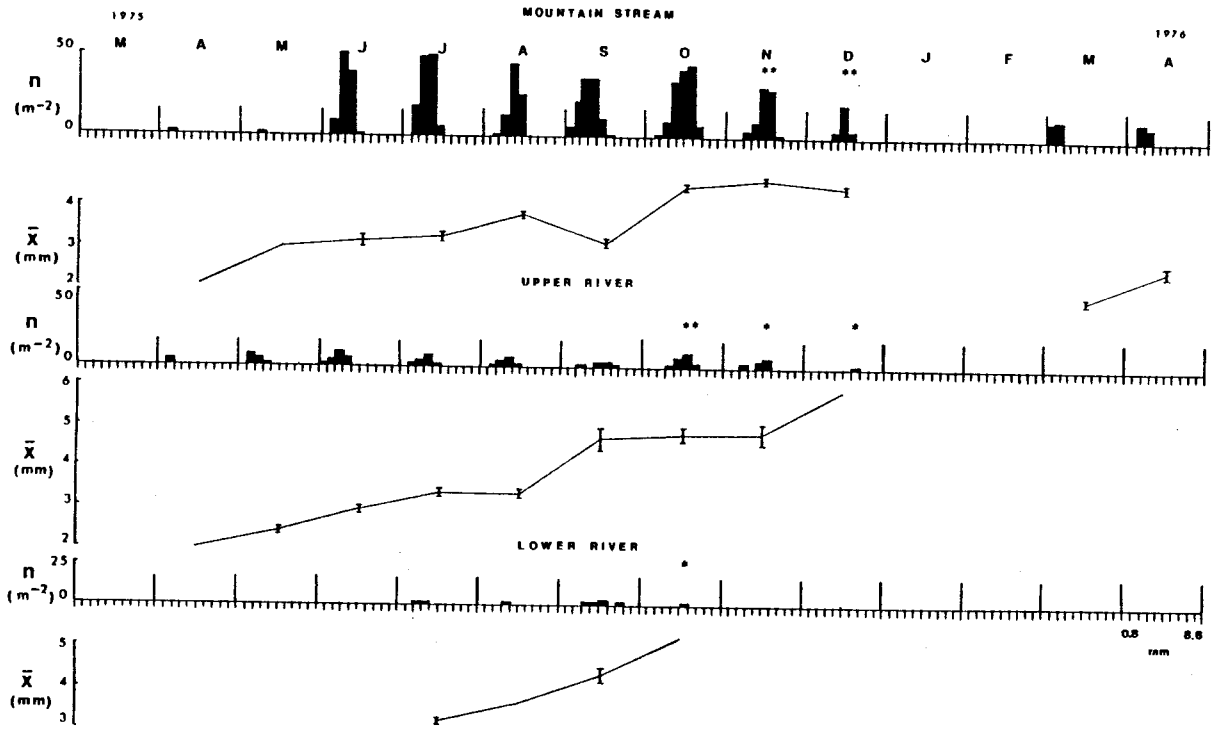

Fig. 3b *Lestagella penicillata.* A winter species that is endemic to the south-western Cape. The life cycle is univoltine and similar to that of *Castanophlebia calida*, but the species is more restricted in its downstream occurrence.

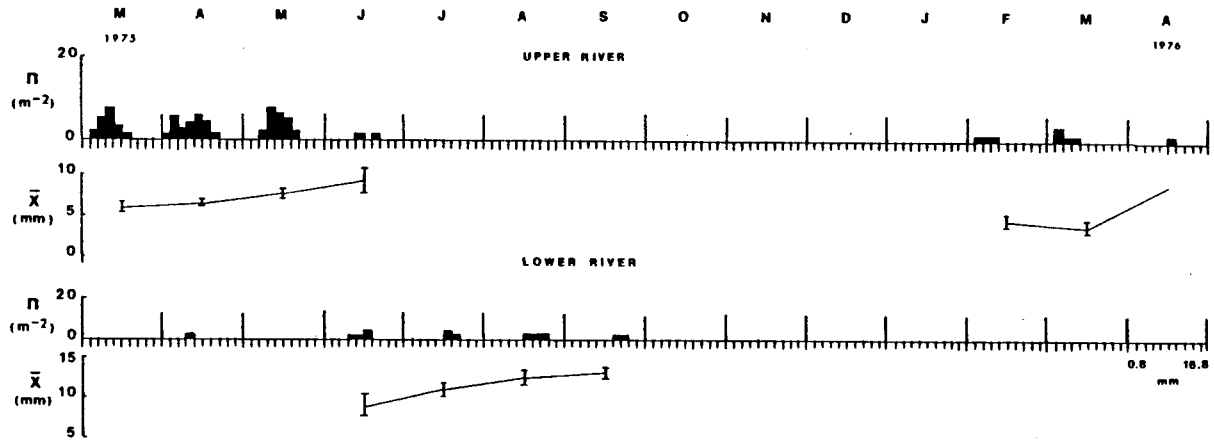

Fig. 3c *Adenophlebia peringueyella.* A summer species characteristically found in the Upper River, and probably endemic to the south-western Cape. The species is thought to be univoltine and appears to grow faster downstream. However, numbers were too low for more conclusive interpretation of the data.

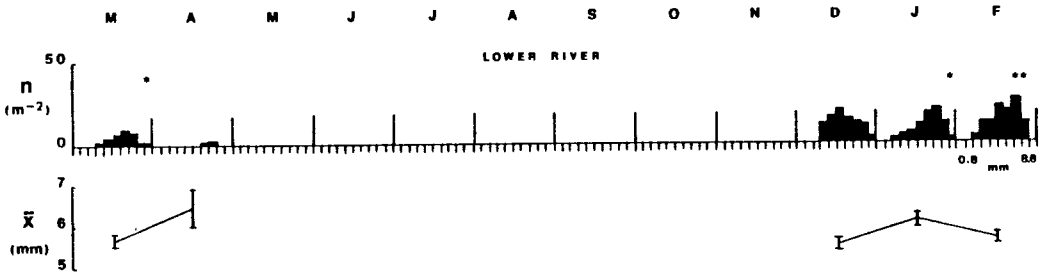

Fig. 3d *Cloeon lacunosum.* A species that occurs year-round in neighbouring lentic waters, but that is restricted in the Eerste River to a summer occurrence in the slow-flowing Lower River zone. Voltinism is probably restricted in the river, though the species appears to produce a succession of hatches throughout the year in still waters.

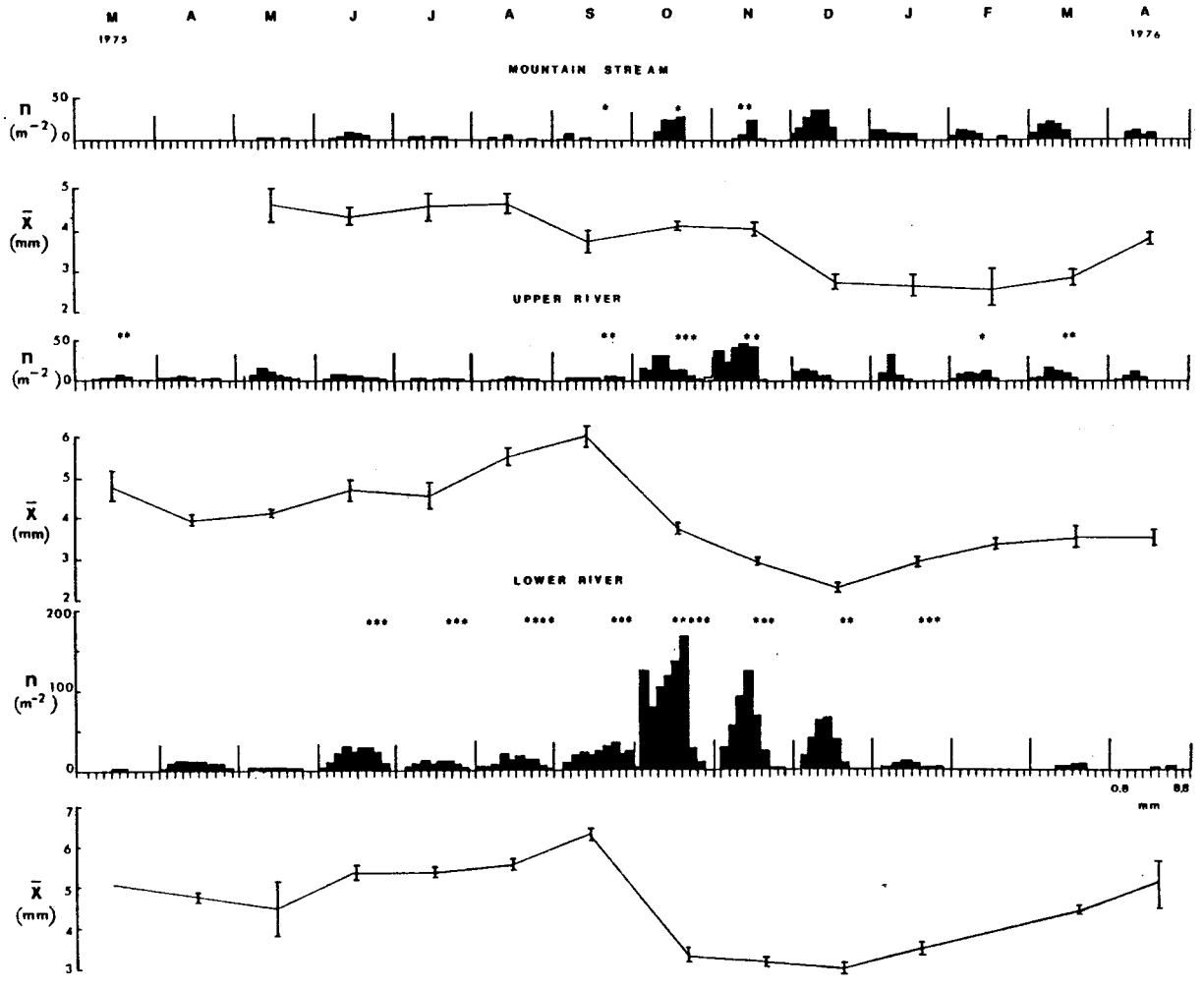

Fig. 3e *Baetis harrisoni.* A hardy species with a flexible life cycle. Production increases markedly downstream, with the species being univoltine in the Mountain Stream, bivoltine in the Upper River, and seemingly multivoltine in the Lower River.

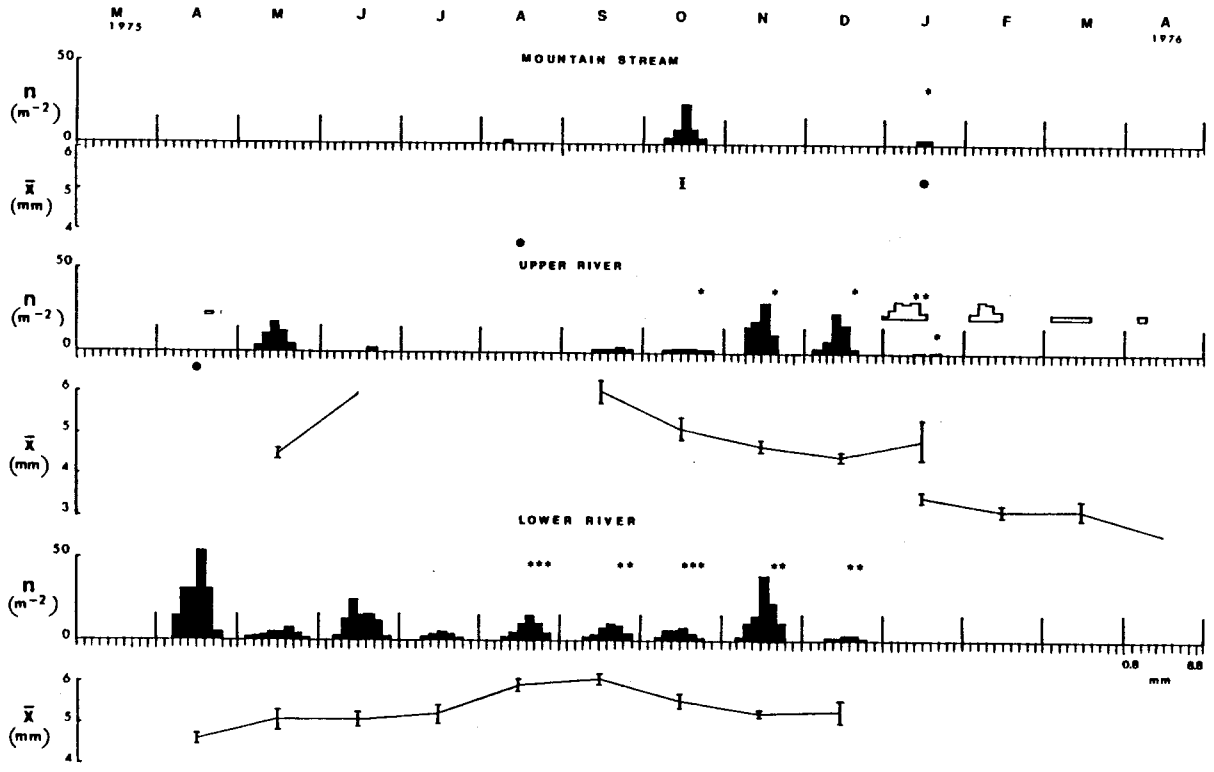

Fig. 3f *Baetis bellus.* A hardy species that is most common in the submerged vegetation of the Lower River. Maturing individuals in the Upper River were forced down onto the stony bed as the water level dropped in summer (unshaded histograms) and the new generation first appeared there, later moving into the vegetation as rains swelled the river. Growth patterns were difficult to interpret and voltinism is uncertain.

Mountain Stream population decreased sharply with the appearance of the new generation. Rates of increase in length and mass of *C. calida*, from their first appearance in May till the first emergences in September, averaged as follows in the three zones:

Mountain Stream	0.05 mm month^{-1}	0.01 mg month^{-1}
Upper River	0.55 mm month^{-1}	0.07 mg month^{-1}
Lower River	0.61 mm month^{-1}	0.12 mg month^{-1}.

Growth of individuals was thus greater further down the river. Once the emergence of adults had begun, the mean lengths of the nymphs became less reliable as a measure of their growth.

Data from this and other studies (Barnard, 1932 1940) suggest that the other species in the winter group are also univoltine, with flight periods occurring in spring and early summer (e.g. *Lestagella penicillata* Fig. 3b). All those species for which sufficient data are available follow the same pattern of growth as *C. calida* growing slowly in the highest zone they occupy, and faster downstream. For instance, rates of increase in length (no data on mass available) of *Ephemerellina harrisoni* were:

Upper River	0.72 mm month^{-1}
Lower River	0.83 mm month^{-1}

and for *Lestagella penicillata* were:

Mountain Stream	0.41 mm month^{-1}
Upper River	0.47 mm month^{-1}.

b) The summer group: The summer species comprise two leptophlebiid species (*Adenophlebia peringueyella*, *Aprionyx peterseni*), two baetids (*Centroptilum excisum*, *Cloeon lacunosum*), one heptageniid (*Afronurus harrisoni*) and one caenid (*Austrocaenis* sp.). Five of the six species occurred on the stony bed and one (*Cloeon lacunosum*) in marginal vegetation. Most were abundant in one zone only, usually the Upper or Lower River, though *A. peterseni* occurred in the Mountain Stream. All were collected principally during summer and autumn, with sporadic appearances of some, usually as large nymphs, during winter and spring. Black wing-buds were recorded only for *Centroptilum excisum* and *Cloeon lacunosum*, so flight periods could not be positively identified in most cases.

The three species of the two upper zones (*Aprionyx peterseni*, *Adenophlebia peringueyella*, *Afronurus harrisoni*) are large animals (up to 14 mm), and are thought to be univoltine. Small nymphs of *Adenophlebia peringueyella* were present in the Upper River in autumn (Fig. 3c), but disappeared from there when the winter rains began. At the same time (June), fewer larger nymphs appeared in the Lower River, remaining and growing there through the winter. No final-instar nymphs were found, but Barnard (1932) and Skaife (1979) give June to October (winter to spring) as the flight period. In this study, no specimens could be found after September until small nymphs were found once again in the Upper River in February. Life cycle data for *Aprionyx peterseni* (Mountain Stream) and *Afronurus harrisoni* (Upper River)

are less complete. Small nymphs of both species were found in late summer and early autumn, and larger nymphs occurred rarely in winter. Once again, no final-instar nymphs were found in this study, but Barnard (1932) suggests a spring and summer flight period for both species. This contrasts with the winter to early spring flight period of *Adenophlebia peringueyella*.

The summer species of the lower River (*Austrocaenis* sp., *Centroptilum excisum*, *Cloeon lacunosum*) are smaller animals (of up to 7 mm), probably with multivoltine life cycles. *Centroptilum excisum* and *Cloeon lacunosum* (Fig. 3d) were present in the Eerste River from early summer to mid-autumn, whilst discharge of the river was minimal. Numbers of both species were highest in mid-summer, when final-instar nymphs were found, then declined as the quality of the water deteriorated. Though absent from samples in winter, both species occur in, and emerge from, quieter waters through the winter (Barnard, 1932), indicating multivoltinism. *Austrocaenis* sp. was similarly most abundant in the river in summer, though rarely common, and was occasionally found in winter. No final-instar nymphs were found, but elsewhere at least, imagos of unidentified species of this genus can be found throughout the year (Barnard, 1932). Calculations of growth rates were impossible for most species because of questionable voltinism, lack of final-instar nymphs, short durations in the river, or low abundances (Table 2). Where calculations were possible, the species usually occurred in only one zone, so comparison of growth rates down the river could not be made. One

species, *Adenophlebia peringueyella*, gave indications of an increased growth rate downstream, growing at 1.07 mm month^{-1} in the Upper River, and later, at 1.34 mm month^{-1} in the Lower River.

c) The hardy group: This group contained four baetid species (*Baetis harrisoni*, *Baetis bellus*, *Acentrella capensis* and *Centroptilum sudafricanum*), which occurred in most of the river throughout most of the year. *Baetis bellus* and *Centroptilum sudafricanum*, characteristically found in marginal vegetation, occurred only rarely in the Mountain Stream, even in winter, when the habitat was available to them. *Baetis harrisoni* and the more rare *Acentrella capensis* were, however, common on the stony bed of that zone. The two species of *Baetis* increased in abundance downstream, while *Acentrella capensis* and *Centroptilum sudafricanum* were most common in the Upper River.

Baetis harrisoni, the most abundant ephemeropteran in the river, increased in numbers downstream, except in late summer to autumn, when it virtually disappeared from the Lower River (Fig. 3e). Its growth and emergence patterns differed in each of the three zones. In the Mountain Stream, half-grown nymphs appeared in May, grew slowly through the winter and began to emerge in September. Mean length of the nymphs ($\bar{x}$) dropped as emergences continued through to November, then dropped again as a new generation of very small nymphs appeared in December. Mean length then increased through the summer and autumn, to reach that of the initial population by the end of the study. In the Upper

River, nymphs larger than those in the Mountain Stream similarly grew through the winter, to emerge between September and November. At the end of the hatch, very small nymphs appeared and grew quickly to produce a batch of smaller final-instar nymphs in February and March. As $\bar{x}$ did not fall appreciably after this (April 1975 & 1976), it seems possible that some individuals remained in the water and joined with those hatching from eggs of the recently-emerged adults, to give the overwintering population.

The population present in the Lower River at the beginning of the study showed a similar increase in $\bar{x}$ through the winter, despite the continual emergence of the largest individuals between June and September. A massive new generation appeared in October, and emergences from much smaller nymphs continued unabated until January. Numbers petered out abruptly in mid-summer, with $\bar{x}$ of the remaining few nymphs increasing by autumn, to the level of the previous autumn. *Acentrella capensis* appeared to follow similar life cycle patterns to those of *Baetis harrisoni*, in the three zones, but the prolonged winter emergences and smaller spring-time generation(s) of the Lower River were missing.

Baetis bellus and *Centroptilum sudafricanum* had similar life cycles. *Baetis bellus*, the more abundant of the two, was rarely found in the Mountain Stream, although on one occasion (October) net sweeps through the marginal palmiet plants did yield high numbers (Fig. 3f). The species was common in marginal vegetation of the Upper River before and after the winter rains, but again

absent from the palmiet during times of high discharge. In summer, late-maturing nymphs were forced onto the stony bed by receding water levels, and very small nymphs were also first recorded there, later moving into the vegetation as the rains began (May 1975). *Baetis bellus* was abundant in the Lower River from mid-autumn to early summer, but absent during the driest months when the physico-chemical quality of the river water was poorest.

In the two lowest zones, mean length of nymphs of *Baetis bellus* increased through the winter, till emergences began in August (Lower River), and October (Upper River). In both zones, final-instar nymphs were then continually present until the species disappeared in summer (Fig. 3f). Voltinism is uncertain, as $\bar{x}$ follows the pattern for a univoltine species (increasing until flight period begins, then decreasing until the species disappears), yet the long flight period and continuing high numbers of nymphs, in the Lower River at least, suggest multivoltinism.

Growth rates of the hardy species were again impossible to calculate in most cases, and have not been attempted.

Emergence phenology

Data on emergences are far from complete. Final-instar nymphs of the summer group of species, for instance, were rarely found. Additionally, significant differences in sizes of final-instar nymphs in the

three zones were difficult to prove due to the low number of such nymphs found. Tests for significant temporal and spatial size differences for multivoltine species were of questionable value anyway, due to their different life cycle patterns in each zone. Nevertheless, some trends are apparent (Fig. 4) and some significant spatial and temporal differences in growth rates of univoltine species did occur. Final-instar nymphs of a typical winter species, *Castanophlebia calida*, appeared first in the Upper and Lower Rivers, and later in the Mountain Stream, with emergence from the Lower River being completed before that from the Mountain Stream began. Final-instar nymphs were significantly smaller ($p < 0.001$) in the highest zone than in the lowest zone and, during the emergence period in any one zone, there was a significant ($p < 0.05$) decrease in size of the nymphs appearing at the final-instar stage. Emergence of another winter species, *Lestagella penicillata*, followed a somewhat different pattern, with final-instar nymphs from the Upper River being larger than those from the Mountain Stream and Lower River, though the differences were not significant. As with *Castanophlebia calida*, however, emergences began first from the Upper and Lower Rivers, and later from the Mountain Stream.

Species of the summer group were each characteristic of only one zone, and were rarely found elsewhere. Final-instar nymphs of some of the species were never found, while those of other species occurred so briefly, compared with the length of the sampling period, that size trends could not be detected. Inclusion of *Adenophlebia peringueyella* and *Cloeon lacunosum* in Fig. 4 illustrates this.

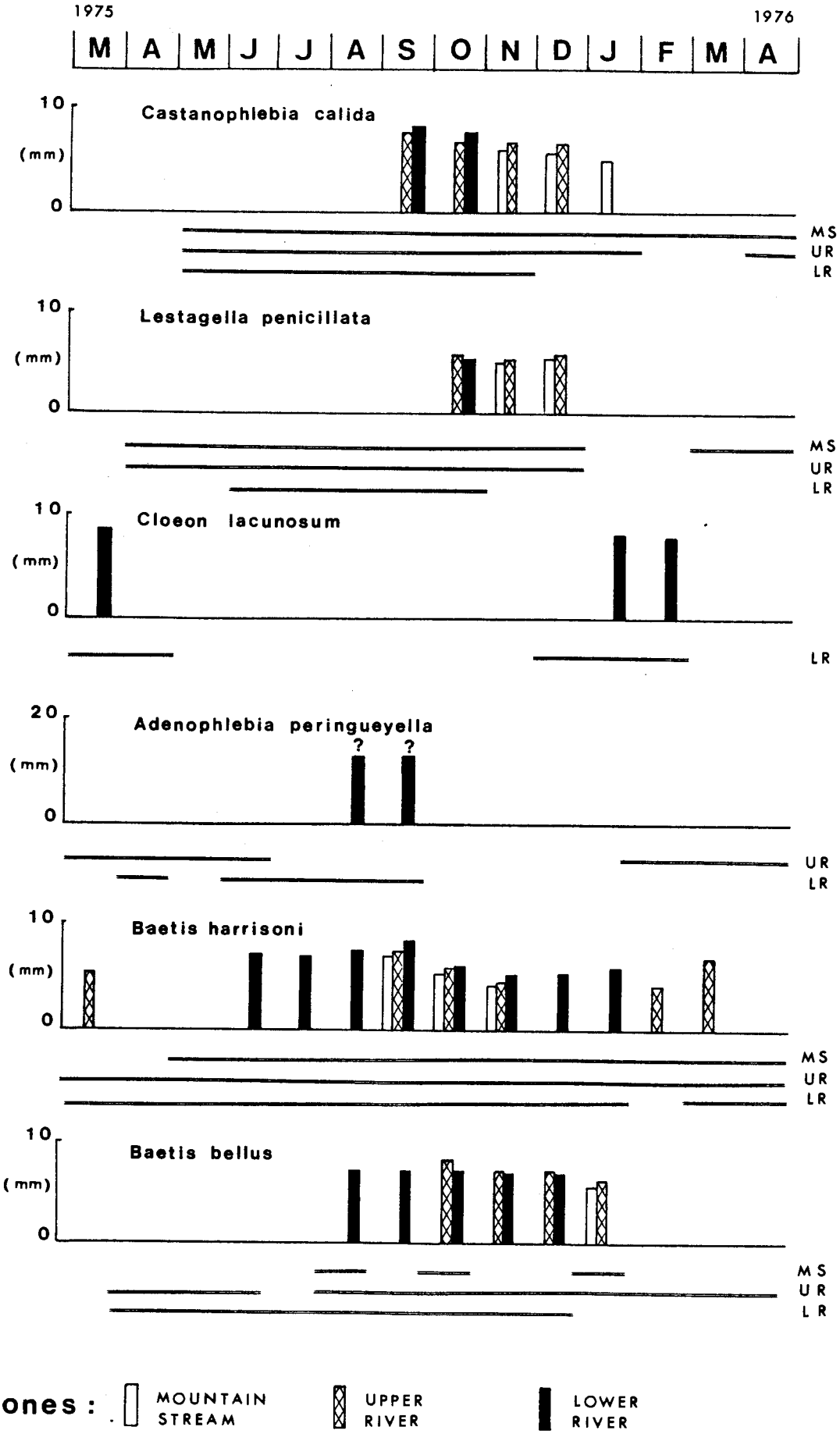

Fig. 4 Mean length of final-instar nymphs in the three zones. Horizontal lines indicate presence of nymphs of any size in samples.

The four species of the hardy group displayed a variety of growth and emergence patterns so statistical comparison of sizes of final-instar nymphs in each zone was not attempted. *Baetis harrisoni* emerged continuously from the Lower River between June and January, with mean size of final-instar nymphs increasing through the winter, decreasing through spring, and increasing again through the summer (Fig. 4), as also did $\bar{x}$ of the total population (Fig. 3e). Adults of *Baetis rhodani* emerging from a river in Germany followed a similar pattern of size changes (Illies, 1979). In contrast, the flight period from the Upper River was split, with a spring-time emergence from successively smaller nymphs, and a late-summer emergence from successively larger ones. A single spring flight period occurred from the Mountain Stream, again with mean size of final-instar nymphs decreasing through the months. *Baetis bellus* emerged from the Lower River over a shorter period than did *B. harrisoni* (Fig. 4), with final-instar nymphs through the months remaining much the same size. Its flight period from the Upper River was shorter and later than that from the Lower River, with mean size of final-instar nymphs generally decreasing in size with time but always being larger than those in the Lower River. A single, small pre-emergent nymph was recorded from the Mountain Stream, late in summer. Trends were not apparent in the two more rare species *Acentrella capensis* and *Centroptilum sudafricanum*), though *C. sudafricanum* appeared to follow similar growth and emergence patterns to those of *B. bellus*. In most cases voltinism of the four hardy species is uncertain, though there is a trend from multivoltinism, or at least bivoltinism, in the Lower River, to univoltinism in the Mountain Stream. The subject is dealt with in the discussion.

DISCUSSION

The Ephemeroptera are numerically important in rivers throughout the world, and as such could play a key role in ecological studies of river systems. Knowledge of the changes in their life-cycle patterns, both along the length of a river and in rivers across a continent, could enhance our understanding of geographical differences in the production and character of rivers, as well as help us pinpoint problem areas in the systems. In this paper I relate distribution and life cycle patterns of the Ephemeroptera in the Eerste River with known patterns over southern Africa, and link data on their growth rates and emergences with literature from abroad. Additionally, I discuss the probable causes for the downstream changes in life cycle patterns exhibited by the group in the Eerste River, and indicate ways in which the simple data presented here can be used to draw basic conclusions on the ecological status of the river.

Interpreting the data has been complicated by three factors: The smallest nymphs and the winged adults could not be collected by the methods used in the general survey, and are therefore not represented in the data; the silt load of the water below the dam construction-site increased during the study, affecting the species composition and abundance of the invertebrates in the highest part of the Upper River zone and thus masking life-cycle patterns; and the total abundance of invertebrates fluctuated greatly during the winter, probably because the animals took refuge deep in the river bed during

spates (King, in press, and see Williams & Hynes, 1974, for relevant references). Monthly abundance figures should be used with caution then, as they indicate only the number of animals on the surface of the substratum and this may have been influenced by the time of sampling in relation to the last spate. Broad trends in distribution and life cycle patterns remained obvious however, and these are discussed below.

Distribution patterns

Distribution of the Ephemeroptera in the river reflects their distribution over the subcontinent. Four winter species (*Ephemerellina barnardi*, *Ephemerellina harrisoni*, *Lestagella penicillata*, *Aprionyx rubicundus*) and three summer species (*Aprionyx peterseni*, *Adenophlebia peringueyella*, *Afronurus harrisoni*) are characteristic of either the Mountain Stream or Upper River zones of the Eerste River. All seven species appear to be endemic to the south-western Cape. *Adenophlebia peringueyella* and *Afronurus harrisoni* have on rare occasions been recorded outside this area, but probably as a result of misidentification - see Schoonbee (1968) and Barnard (1932, 1940). All but these two species - which should probably be included - are listed by Harrison & Agnew (1962) as 'Table Mountain Sandstone acid-water species'. They form part of the unique aquatic fauna restricted to headwaters of rivers in the south-western Cape. The same small geographic area supports fynbos, a unique, indigenous heath-like vegetation that is extremely rich in species. The unspoilt headwaters running through fynbos are acidic, brown-stained and low in

productivity. Such headwaters are endangered habitats, due to the manipulation of the catchments to produce ever more water for this drought-prone area.

Three of the four hardy species (*Baetis harrisoni, Baetis bellus, Centroptilum sudafricanum*), three winter species (*Castonophlebia calida, Choroterpes elegans, Pseudocloeon vinosum*) and one summer species (*Centroptilum excisum*) occur widely over the subcontinent. Most also occur throughout the river, or are more common in its lower reaches. They are either not pH-sensitive, or tend to be present in alkaline waters (Harrison & Agnew, 1962). The three hardy species are an important component of riverine fauna throughout the country (Crass, 1947; Harrison, 1965; Noble, 1970) and are part of the southward-invading Pan Ethiopian fauna which now constitutes the bulk of the South African riverine invertebrates (Harrison, 1965). *Castanophlebia calida*, the most common of the three winter species, is abundant in the eastern Cape (Crass, 1947), and occurs at high altitudes in Natal (Oliff & King, 1964). It is a typical remnant of the Mesozoic fauna of the subcontinent, which is now limited to montane regions except in the temperate south-western Cape (Harrison, 1965) (See also Sweeney & Vannote, 1978). Its seasonal appearances in winter in the Cape (a winter rainfall area) and in summer in Natal (a summer rainfall area) suggest a need for fast-flowing rivers as well as cool water. Another of the winter species *Choroterpes elegans*, in contrast to *Castanophlebia*, must be near the geographical limits of its range in the south-western Cape. It is present but rare in the Eerste and nearby Berg Rivers (Harrison & Elsworth,

1958), but plentiful over the remainder of the country (Barnard, 1932; Crass,1947; Harrison, 1958; Allanson, 1960; Chutter, 1963; Agnew, 1965; Oliff *et al.*, 1965; Noble, 1970). It can probably be included in the Pan Ethiopian fauna. *Pseudocloeon vinosum*, also tentatively a winter species, was rare in the Eerste River, common year-round in the nearby Berg (Harrison & Elsworth, 1958), present in the Vaal River in Transvaal (Chutter,1970) but absent from Natal and the eastern Cape (Crass, 1947). This odd distribution pattern needs further investigation. Presence of the last of the widespread species, *Centroptilum excisum*, is also varied, for it is a typical summer animal in the Eerste River, predominantly a winter animal in Natal (Crass, 1947), and occurs year-round in the Transvaal (Chutter, 1970).

Two summer species (*Austrocaenis* sp. and *Cloeon lacunosum*) and one hardy species (*Acentrella capensis*) appear to be neither widespread over the country nor restricted to acid headwaters of the area. Such a distribution pattern may, however, be due to insufficient sampling, especially in western South Africa, or to the difficulty of identifying to species. The taxonomy of *Austrocaenis* for instance, is poorly known, with reported occurrences restricted to generic level. *Cloeon lacunosum* appears to occur only in a very restricted area around Cape Town, and has not been reported from the Berg River (Harrison & Elsworth, 1958; Coetzer, 1978). 'Lower River' or 'still water' species are usually quite hardy and widespread, so a closer study of this reportedly ovoviviparous mayfly (Barnard, 1940) would be interesting. *Acentrella capensis* has only been reported

from the south-western Cape, yet it is not restricted to acidic headwaters of the region, for it occurs in low numbers throughout the stony-bed reaches of both the Berg (Harrison & Elsworth, 1958) and Eerste (King, in press) Rivers.

Life cycles and emergence patterns

Hynes (1970) has summarised the information on life histories and seasonal cycles of riverine invertebrates known at that time. Many of the phenomena he discusses pertaining to life cycles and growth rates of the animals are apparent in the Ephemeroptera in this study. Their life cycles range from uni- to multi-voltine. At least one species (*Baetis harrisoni*) has a univoltine life cycle in the Mountain Stream, a bivoltine one in the Upper River and probably a multivoltine one in the Lower River (all within a 15 km stretch of river). *Baetis rhodani*, a widespread European species, also dispenses with its summer generation in high, cool streams (Pleskot, 1958, 1960, in Hynes 1970), but produces up to three winter and three summer cohorts in an Austrian stream flowing from a high-altitude lake (Humpesch, 1979).

Although our knowledge of local species is incomplete and the more rare species can be classified only provisionally into uni- or multivoltine groups, some characteristics of these two groups are nevertheless obvious. Species occurring only in the cold, fast-flowing waters of winter and spring, and those summer species

restricted to the two cooler, upper zones, generally have univoltine life cycles, are acid-water species and are endemic to the area (Table 2). *Castanophlebia calida*, while not meeting the last two specifications, still displays univoltinism in the Eerste River. The two other non-endemic winter species *Choroterpes elegans* and *Pseudocloeon vinosum*, may similarly display univoltinism, but were too rare for satisfactory interpretation of the data. Proposed univoltinism of two other species from this group contradicts previous records: the two peaks of emergence of *Afronurus harrisoni* (Barnard, 1932) now seem certain to be due to misidentification of two similar species (Schoonbee, 1968), while the 'successive hatches' of *Aprionyx peterseni* (Barnard, 1932) seem strange, considering the large size of the nymphs (up to 14 mm excluding cerci), and their presence only in headwaters of low productivity.

Species of the multivoltine group occur throughout the river for most of the year, or in the slow-flowing, polluted water of the lower reaches in summer. They are generally distributed widely over the country, are less specific in their environmental needs than the previous group and have multivoltine life cycles. Exceptions are *Acentrella capensis* and *Cloeon lacunosum*, which may not be widespread, and *Centroptilum excisum*, for which multivoltinism has not been proven. It seems likely that for *Centroptilum excisum* and for *Cloeon lacunosum* conditions in the Eerste River permit only one late summer - early autumn generation, while in cleaner and more tranquil waters, emergences (and thus probably a succession of

generations) continue through more of the year (Barnard, 1932).

Flexibility of life cycles of Ephemeroptera is well documented (Hartland-Rowe, 1964; Hynes, 1970; Newell & Minshall, 1978; Sweeney, 1978; Humpesch, 1979; Vannote & Sweeney, 1980). Temperature is a major influencing factor, and probably interacts with day length to control the time of emergence (many insects emerge earlier at lower altitudes and lower latitudes) and the length of the emergence period (which may be shorter at lower altitudes - Hynes, 1970). Vannote & Sweeney (1980) have shown that annual degree day accumulation is a function of latitude for rivers in the United States. They suggest that an 'optimum' thermal regime exists where adult size and fecundity of insect species are maximized, and that temperature regimes warmer or cooler than the 'optimum' result in smaller less fecund adults. The Lower River zone of the Eerste River (Lat. 34°S), with roughly 6400 degree days per annum, agrees with their projection of latitude vs. degree days, while the Upper River and Mountain Stream accumulated 5800 and 5200 degree days respectively. The different growth rates of Ephemeroptera in these three zones could be due to the annual accumulation of 23% more degree days in the Lower River than in the Mountain Stream, and 10% more in the Lower River than in the Upper River. The winter mayflies, then, which grow fastest and largest in the Lower River (e.g. *Castanophlebia calida*) would, according to Vannote & Sweeney, be closest to their optimum conditions there, while species such as *Lestagella penicillata*, which grow fastest and largest in the Upper

River, would be closer to their optimum conditions in the upstream cooler water. However, the degree days accumulated in the much shorter period that is actually available to these mayflies between their initial appearance (May) and their first emergences from the Lower River (September) (Fig. 3a, 3b), were approximately 1680 (Mountain Stream), 1840 (Upper River) and 1940 (Lower River). Due to the short length and fast flow of the river, downstream increases in water temperature were smaller in winter than over the whole year, the Lower River accumulating only 15% more degree days than the Mountain Stream and 5% more than the Upper River in that time. Nevertheless, the growth rates of many species were twelve times greater in the Lower River than in the Mountain Stream, during winter (see *Castanophlebia calida* Fig. 3a, for instance). It is not known to what extent the downstream increases in water temperature could account for such differences.

Anderson and Cummins (1979) showed for the collector-gatherer midge *Paratendipes albimanus* (which appears to feed in the same way as *Castanophlebia calida*), that food quality always outweighed the direct effect of temperature on larval growth. The fynbos vegetation of the upper catchment of the Eerste River is tough-leaved, evergreen shrub which produces relatively little leaf litter (unpub. data), while the Mountain Stream itself is very low in nutrients and almost without aquatic macrophytes (King, 1981). Conditions for growth of a detritivore there compare unfavourably with those of the Lower River, where abundant leaf litter from mixed evergreen and deciduous trees falls continuously into the

already nutrient-rich water. *Castanophlebia calida* could be growing fastest in the Lower River (Fig. 3a) at least partially because of the greater availability of food there. Laboratory experiments have indicated that it is the scarcity of food in the Mountain Stream rather than the lower water temperature or nature of the allochthonous detritus there, that is responsible for the very slow growth rates of the Mountain Stream population (unpub. data). *Baetis harrisoni* could be showing a different kind of response to downstream increases in the quantity of available food, by producing more generations in the lower reaches than in the Mountain Stream (Fig. 3e).

Quality and quantity of food and temperature, then, both can affect the growth rates, and thus the voltinism, of aquatic insects. Life cycles of the Ephemeroptera in the Eerste River illustrate the difficulty of separating the effects of the two, but also indicate that whatever the cause, secondary production in the river increases markedly downstream. While species with univoltine cycles display this increase by growing faster and larger downstream, those with multivoltine cycles may additionally produce more generations in the lower reaches.

Knowledge of these life cycles can help us locate problem areas in rivers, which may not be detectable by chemical analyses of the water. The animals will only be present in a river if conditions there continually meet their needs. Presence of almost-

mature individuals of univoltine species such as *Castanophlebia calida* and *Lestagella penicillata* in a river in spring, for instance, indicates that conditions there have been favourable for their survival throughout the preceding autumn and winter. Absence of the univoltine species *Afronurus harrisoni* from the river below the dam site, after a massive input of silt briefly covered the stony bed, mutely recorded the event long after the physical evidence had disappeared. The species (and many others) could only re-inhabit the area in any great number the following year, when eggs laid by adults emerging elsewhere, hatched. Common ephemeropterans, such as *Castanophlebia calida* and *Baetis harrisoni*, could possibly be used as indicators of the level of production along rivers. While confusion remains concerning the relative importance on secondary production of influencing factors such as temperature and food, it may be possible to by-pass the causes and measure the effects, to give a simple indication of the total production potential of a stretch of river.

I conclude that the distribution and life cycle patterns displayed by the Ephemeroptera of the Eerste River follow trends that have been detected in aquatic insects in many parts of the world. The group is an important component of the local riverine fauna, and is clearly very sensitive to changing conditions in the river. While much remains to be investigated, the ephemeropterans of stony-bed streams, with their variety of life-cycle responses to their environment, have great potential as indicators of changing physico-chemical conditions and productivity levels.

SUMMARY

1. A study of the stony-bed reaches of the Eerste River in the south-western Cape Province, South Africa, has revealed 17 species of Ephemeroptera, with the Leptophlebiidae (5 spp) and Baetidae (7 spp) being the dominant families.

2. Spatial changes in species and abundance of Ephemeroptera along the river reflected the changing physico-chemical condition of the water, with a general summertime decrease in species downstream. Temporally, most species occurred mainly in the dry summer and autumn, or the wet winter and spring, with the seasonality of occurrence least obvious in the headwaters, and increasingly more obvious downstream.

3. Many of the species had univoltine life cycles, while the remainder displayed life cycles which varied in response to environmental conditions. Several of the latter group had univoltine cycles in the headwaters and bi- or multivoltine cycles in the lower reaches.

4. Those species with univoltine cycles were 'winter' species or 'summer' species of the higher reaches, only occurring in cool and clean, or at least well oxygenated, water. Most are endemic to the south-western Cape Province.

5. The species with more flexible cycles are generally hardier species, and occurred throughout the river, or in the polluted lower reaches in summer. Most of these hardy species occur widely over the subcontinent.

6. Increasing levels of productivity down the length of the river were displayed by both groups. While species with univoltine cycles grew larger and faster downstream, some with multivoltine cycles additionally produced more generations in the lower reaches.

7. It was impossible to distinguish the separate effects of changes in water temperature and food availability on the animals. It was felt, however, that both are strongly involved in producing the variety of life cycles displayed by the Ephemeroptera, and the increase in their productivity down the river.

ACKNOWLEDGEMENTS

My sincere thanks to Professor George Branch and Doctors Bryan Davies and John Agnew, who critically read various drafts of the paper. The research was financed by the Council for Scientific and Industrial Research and the University of Cape Town.

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PART 4

ALLOCHTHONOUS DETRITUS AND GROWTH RATES OF A BENTHIC DETRITIVORE IN A SMALL SOUTH AFRICAN RIVER

ALLOCHTHONOUS DETRITUS AND GROWTH RATES OF A BENTHIC DETRITIVORE IN A SMALL SOUTH AFRICAN RIVER

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ABSTRACT

The southern and south-western Cape Province of South Africa support fynbos, an heath-like vegetation, and mountain streams running through this vegetation are low in productivity. As such streams appear to be heterotrophic, with litter from fynbos thus forming a major source of their energy, the dynamics of allochthonous detritus in a mountain stream and in a downstream, more productive stretch of the same river were compared, to ascertain what influence fynbos has on secondary productivity of the stream.

Biomass of litter from evergreen riparian trees in the fynbos biome (2,68 t ha^{-1} yr^{-1}) was about half that of downstream deciduous trees (4,59 t ha^{-1} yr^{-1}). The sclerophyllous fynbos leaves leached and decayed as quickly as did the deciduous leaves, and were as palatable to aquatic detritivores. Allochthonous detritus on the river bed thus disappeared equally quickly from both stretches of river but, because of the lower input from fynbos vegetation, it was always more scarce in the mountain stream.

The life cycles of most of the invertebrate species in the mountain stream are annual autumn-to-summer ones, yet peak litter-fall of the riparian fynbos vegetation is in mid-summer and most of this litter has disappeared from the river bed by late autumn. The animals thus do not exploit peak input of the sparse amount of litter entering the stream, and food is scarce through the greater part of their lives. Growth experiments with a riverine detritivore, the ephemeropteran *Castanophlebia calida*, suggest that it is this scarcity of food that is responsible for the low secondary productivity of the mountain stream.

1. INTRODUCTION

The southern and south-western tip of South Africa supports a unique vegetation known locally as fynbos (pronounced fane-bos), which covers roughly 41 000 km² (Kruger, 1979). Equivalent to the macchia of the Mediterranean region, the chaparral of California, the matorral of Chile and the heath of Australia, fynbos occurs as sclerophyllous shrubland and heathland, and is exceptionally rich in species. With the botanical rank of Kingdom, it has equivalent botanical status to very large areas, such as the whole of the temperate and arctic northern hemisphere (Taylor, 1979).

Much of the fynbos has disappeared with urban and agricultural development of the region, but stands of undisturbed mountain fynbos are still present in mountain catchments. These catchments are formed of hard, quartzitic rocks which produce shallow, acid, leached soils, and the fynbos supported by such soils grows slowly (Day, in press). Fynbos on the slopes, characterised by three physiognomic groups - proteoid, restioid and ericoid - gives way to riparian communities in river valleys. Riparian trees are small and evergreen, with most species confined to the fynbos biome (Palgrave, 1977). The highly potable water in the mountain streams is acid (pH 4,3 to 6,8 in different streams), brownstained and very low in nutrients (King, *et al.*, 1979). The scarcity of aquatic plants in such streams, and the presence of leafy canopies over the water, suggest that the streams are heterotrophic, with fynbos thus exerting a considerable

influence on their secondary productivity, which is generally acknowledged to be low (Noble & Hemens, 1978; King, 1981).

It seems likely that the sclerophyllous nature of the leaves of fynbos species precludes their early decomposition in water, and the secondary compounds they contain may render them unattractive as food for detritivores. Additionally, the acid, nutrient-poor waters of the mountain streams may suppress activity of microbial decomposers (Kaushik & Hynes, 1971), further slowing the decomposition process. All these factors may result in a poor foundation for the aquatic food web in the stream.

The investigations described here were designed to test some of the above assumptions, in a first attempt to identify the reasons for the low productivity of the mountain streams. As these streams appear to be heterotrophic, and thus largely dependent on terrestrial vegetation for their energy, investigations initially focussed on ascertaining and comparing the quality and quantity of allochthonous detritus entering the mountain stream and lower reaches of a local river, the Eerste River. With the two major contributors of allochthonous detritus at each section of river identified, rates of decomposition of their leaves were compared by measuring their leaching rates in the laboratory, and by recording loss of mass with time, from bags of their leaves placed in a mountain stream. The degree of skeletonisation of the leaves after submersion in the stream indicated the relative attractiveness of the four major species as food for aquatic detritivores.

Feeding experiments were then conducted in the laboratory, using a common riverine detritivore, the ephemeropteran *Castanophlebia calida* Barnard. The rate of turnover of this species has been shown to be much lower in the mountain stream than in the lower reaches (part 3). An initial experiment was undertaken to measure growth of *C. calida* at temperatures that were representative of the mountain stream or lower river, in order to ascertain the effects of natural downstream increases in water temperature. In two further experiments the growth of this species was measured while it was on a diet of either fynbos leaves or deciduous, exotic leaves, at various levels of food availability, to ascertain if growth differed with different types of food and if it increased with an increase in available food.

2. THE STUDY AREA

The area, river and physico-chemical quality of the water of the Eerste River have been described in King (1981). Briefly, the 40 km long river (33°55'S, 19°00'E) has a 400 km² catchment, which lies entirely in the winter rainfall area of South Africa (Fig. 1). During the study, discharge of river water reached its maximum of 36,5 m^3 sec^{-1} in winter (June - August), when more than 80% of the annual rains normally fall, and its minimum of 0,3 m^3 sec^{-1} in summer (December - February), when rainfall is negligible. Annual water temperatures ranging between 10° and 28°C were typical of the area. The three physical/biotic zones of the river recognised in King (1981) were a Mountain Stream zone in undisturbed mature fynbos, a Lower River zone in agricultural land with deciduous, exotic riparian trees, and an intermediate Upper River zone which was transitional between the two. All three zones had a stony substratum.

One station in the Mountain Stream (station A) and one in the Lower River (station B) were chosen for the present study, representing sites where secondary production of aquatic macro-invertebrates is known to be markedly different (King, 1981; in press). Station A (station 1 of original study) was situated at 382 m above sea level, in the undisturbed mountain stream, where the river water is clear-brown, unpolluted and poorly buffered, with a pH between 5,8 and 7,1. Small riparian trees, all indigenous and evergreen, form a sparse but

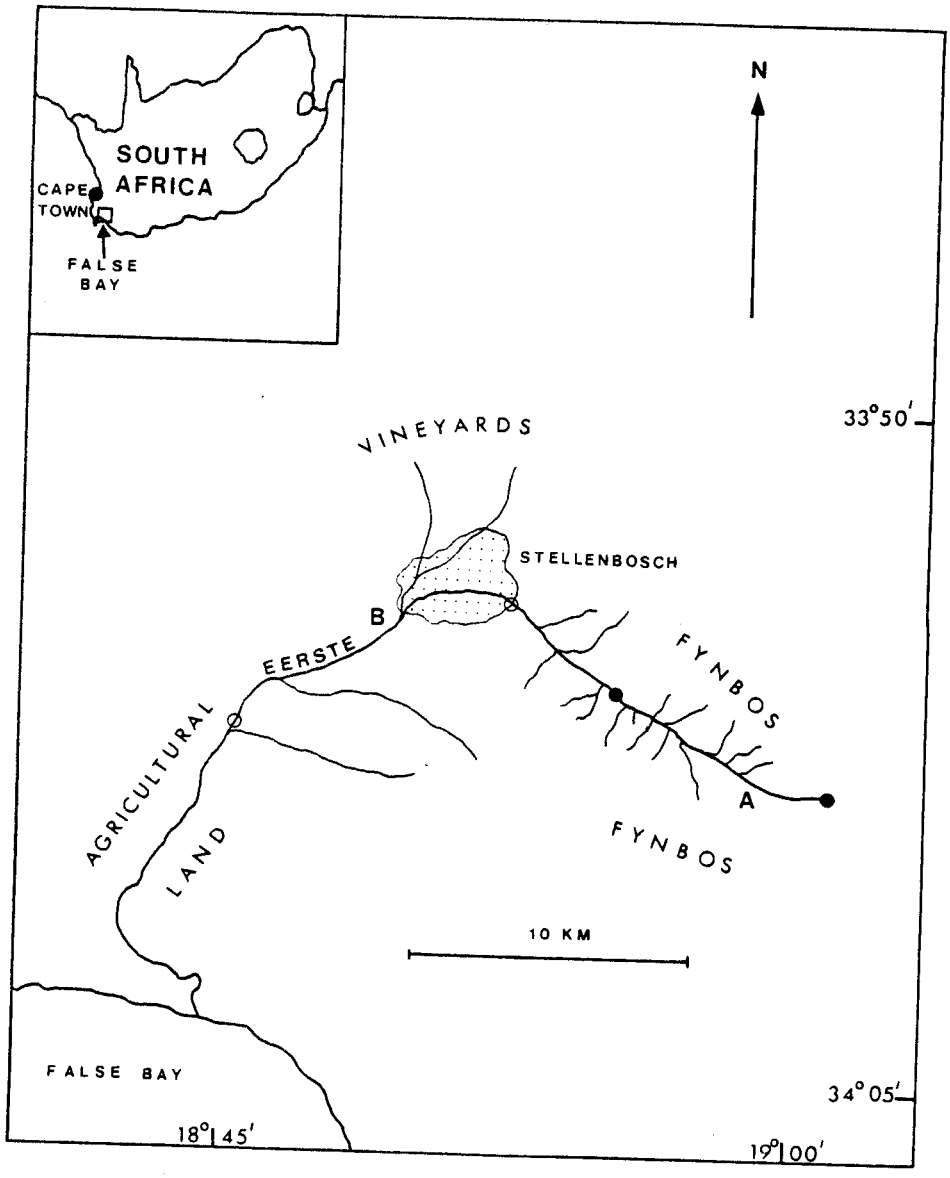

Fig. 1 The Eerste River, showing the river zones (Mountain Stream ● to ● ; Upper River ● to ○ ; Lower River ○ to ○), and the sampling stations A and B.

almost continuous canopy over the 5 - 7 m wide river. Aquatic macrophytes are confined to marginal clumps of palmiet *Prionium serratum* and, rarely, a small *Scirpus* species trailing from mid-river boulders. Rocks on the river bed sometimes feel slippery, but support no obvious plants other than the *Scirpus*.

Station B (station 4 of original study) was 18 km downstream of station A, at an altitude of 77 m above sea level. By this point the river has flowed through foothills covered with vineyards, and then through the winery-orientated town of Stellenbosch. The river water is well buffered (pH 6,8 - 8,8) and contains many pollutants. A belt of mixed deciduous and evergreen trees, all exotic, occurs on each bank. The trees, much taller than those at station A, form a canopy over the 8 - 18 m wide river in places. Marginal vegetation (reeds, grasses) is abundant, and filamentous algae and sewage micro-organisms appear on the rocky river bed in summer. Despite the degradation of these lower reaches and the drastic deterioration in water quality each summer, the river there is in reasonable condition in winter, due to scouring and dilution by powerful spates. Though still high in nutrients, the water is sufficiently clean and well-oxygenated in winter for some invertebrate species to extend downstream from station A to station B and beyond, but in summer, zones of different groups of species are markedly delineated down the length of the river.

3. METHODS

3.1 ALLOCHTHONOUS DETRITUS

The quality and quantity of allochthonous detritus entering the river was recorded by suspending six litter traps, with a total opening area of 1 m^2 above the banks at both stations A and B. Litter was collected monthly between May 1978 and May 1979, sorted to species, oven dried at 60°C for 24 h, and then weighed.

At the same stations, detritus on the river bed was collected monthly between February 1978 and May 1979. A square frame with sides 25 cm was placed on the river bed, and all the vegetative litter within it collected. Four such samples were pooled to give a monthly sample for each station, and these samples were treated in the same way as those from the litter traps.

Leaves of two fynbos species, *Brabejum stellatifolium* and *Metrosideros angustifolia*, and of two deciduous exotic species, *Populus canescens* and *Quercus robur*, were used in all experiments on leaching and decomposition. These species are respectively the two main contributors of fynbos leaves at station A, and of deciduous leaves at station B. Leaves which were about to fall were collected from the four species during late summer and autumn 1982; only autumnal-coloured leaves that dropped from the trees when touched, were used.

Plate 1. Litter bags containing leaves of the four experimental species, before submersion in Window Stream. Three replicates for each species were prepared, using both fine-mesh bags (light coloured) and coarse-mesh bags (dark coloured). The 24 bags were stapled to a wooden plank and then secured by a covering of coarse-mesh netting.

Plate 2. The planks with the litter bags were secured in Window Stream in such a way that the bags hung down into the water and were in contact with the substratum.

stream on the slopes of Table Mountain, and is roughly equivalent to the Mountain Stream zone of the more-distant Eerste River. Bags of two different mesh sizes were used so that the aquatic invertebrates either could be kept away from the leaves (0,5 mm aperture size) or could enter the bags (3 - 4 mm aperture size). The effect of the fauna on the decomposition processes thus could be ascertained. Between 1 and 2 g of dried leaves of a single species were placed in each bag, the four species having three replicates in each kind of bag (a total of 24 bags). The bags were stapled onto a wooden plank in such a way that when the plank floated they hung down into the water in a closely-packed cluster (Plate 1). Seven such planks were prepared, a total of 168 bags, and these were placed in Window Stream so that the bags were in contact with the substratum (stream depth is a few cm). Each plank was securely attached to several immovable objects, using nylon fishing line (Plate 2). One plank was lost in a spate; the others were collected at 2, 4,5, 7, 9,5, 12 and 15 weeks from the beginning of the experiment, which lasted from mid-autumn (April) to late winter (August).

3.2 GROWTH EXPERIMENTS

Preliminary investigations of the biology of *Castanophlebia calida* were conducted to discover its requirements for life in a tank. Twelve almost-mature nymphs of *C. calida* were collected from station A in January 1978, and their gut contents analysed. The results

indicated that the species is detritivorous, and nymphs in captivity were seen to feed on the surface layers of dead leaves (further details in Results). The ability of the nymphs to survive without the leaves was investigated by placing 20 nymphs in each of two tanks in a darkened room. The tanks contained only stones and river water, and air was bubbled through the water. One tank was left untouched throughout the 15 days of the experiment, while the sides of the other tank and the stones it contained were scrubbed clean of slime each day. Mortality of the nymphs in the two tanks was recorded.

All experimental work with *C. calida* had to take place between May when the young nymphs are sufficiently developed to be positively identified and sexed, and September when emergences of imagos was likely to commence. The experiments, which involved measuring growth, were stopped as soon as the first sub-imago emerged, as mean size of the remaining (smaller) nymphs in that tank would then be lowered, making comparisons between tanks less valid. Measurements of lengths of live nymphs, from the anterior of the head to the base of the cerci, were made using a dissecting microscope with an ocular micrometer. Identification of sexes was based on development of the compound eye, as even very small male nymphs bear the darkened triangles between their eyes that will eventually swell to form the turbinate eye of the mature male.

The experimental tanks measured 40 cm x 25 cm and were 12 cm deep. For the feeding experiments, two scrubbed stones from the river bed

were placed in each tank to provide shelter for the nymphs, since they are typically found clinging to the underside of stones of the river bed. Freshly-collected water, which was changed weekly, was added to cover the stones, and air was continuously bubbled into the tanks. Brown paper covered all windows of the experimental rooms, to give a dim light in which algae could not grow.

In the first feeding experiment, which involved measuring growth attained at two different temperatures, leaves of the four tree species were leached for one week in river water and then dried. Various amounts of dried leaves, totalling 4 g (Table 1), were then placed in the prepared tanks and left in the water for one week to initiate decay; after this 20 measured nymphs of *C. calida* were placed in each tank. Leached leaves were used because the soluble substances are quickly washed from the leaves on submersion, leaving only the less soluble elements remaining available to the aquatic invertebrates over an extended period. The experiment ran from 28 July to 19 September 1978, when the first sub-imago emerged, and all surviving animals were then re-measured.

In the second feeding experiment, which involved measuring growth attained at various levels of food availability, leached leaves were added to 12 prepared tanks as per Table 2, and all the tanks were kept at the same temperature of 15°C. Six tanks held various amounts of fynbos leaves, while the other six held similar quantities of leaves from the exotic species. The ratio of the mass of leaves of the two species of plant in each tank was roughly the same as their

TABLE 1 Contents of experimental tanks and temperature of water for the first feeding experiment.

	Tank Number and Label	Water Temperature (°C)	Leaves Placed in Tank (g dry mass)
Fynbos	1		
	2 replicates	10	*Brabejum* 3 g *Metrosideros* 1 g
	3		
Exotic	4		
	5	10	*Populus* 3 g *Quercus* 1 g
	6		
Fynbos	7		
	8	15	*Brabejum* 3 g *Metrosideros* 1 g
	9		
Exotic	10		
	11	15	*Populus* 3 g *Quercus* 1 g
	12		

TABLE 2 Contents of experimental tanks for the second feeding experiment

Tank Number and Label		Leaves Placed in Tank (g dry mass)				Total Mass of Leaves (g dry mass)
1		0,04 *Metrosideros*		0,09 *Brabejum*		0,13
2		0,12	"	0,38	"	0,50
3	Fynbos	0,25	"	0,75	"	1,00
4		0,50	"	1,50	"	2,00
5		0,75	"	2,25	"	3,00
6		1,00	"	3,00	"	4,00
7		0,04 *Populus*		0,09 *Quercus*		0,13
8		0,12	"	0,38	"	0,50
9	Exotic	0,25	"	0,75	"	1,00
10		0,50	"	1,50	"	2,00
11		0,75	"	2,25	"	3,00
12		1,00	"	3,00	"	4.00

ratio on the river bed (Fig. 2). Calculations of the total mass of leaves that were placed in each tank were based on previous knowledge of the density of *C. calida*, and of the quantity of allochthonous detritus at stations A and B (part 3 and this part). At station A, for instance, the mean abundance of *C. calida* in winter was 284 individuals m^{-2}, and the average amount of detritus on the river bed during that period was 6,27 g dry mass m^{-2}. Thus 20 nymphs would have had a maximum of 0,44 g dry mass of detritus available to them (in reality, the figure would have been much lower, due to the presence of other detritivores). Similarly, 20 nymphs at station B would have had a maximum of 3,68 g dry mass m^{-2} of detritus available to them. The range of food levels in the tanks, from 0,13 to 4,00 g dry mass, encompassed these extremes.

Leaves were conditioned in the tanks for one week, and then 20 measured nymphs of *C. calida* were introduced to each tank. The experiment ran from 9 July to 4 September 1979, when the surviving animals were re-measured.

4. RESULTS

4.1 THE ALLOCHTHONOUS DETRITUS

Detailed below are the quantities of litter that fell from riparian trees, the species composition of this litter and the fluctuations in its biomass through the year. The mass and nature of the litter lying on the river bed during the same months is compared with that that fell from the trees. Results of experiments dealing with leaching and decomposition of the litter are then used to indicate the likely fate of leaves that fall into a western Cape stream.

Annual litter-fall at station B was almost twice that at station A (Table 3). At both stations the soft litter (leaves, fruit, flowers etc.) comprised the major proportion of the litter, while stem litter (twigs, bark etc.) made a very minor contribution. Even so, stem litter at station B (12% of total litter) was considerably higher than at station A (3%). Composition of the litter on the river bed differed from that in the litter traps (Table 3). The proportion of leaves dropped, while that of twigs and bark increased five to seven-fold. The change was most noticeable at station B, where the proportion of soft litter on the river bed (28%) fell dramatically compared with that in the litter traps (87%). For station A, the annual mean standing stock of all litter in the river was almost the same as the total annual litter falling from the trees (Table 3), and

TABLE 3 Nature and quantity of total litter collected in litter bags and from the river bed during the study.

STATION	Litter Bags t ha^{-1} yr^{-1}				River Bed t ha^{-1} (monthly average)			
	Leaves, fruit, flowers	Wood, bark	Acorns	Total litter	Leaves, fruit, flowers	Wood, bark	Acorns	Total litter
A (fynbos)	2,60 (97%)	0,08 (3%)	-	2,68	2,07 (78%)	0,59 (22%)	-	2,66
B (exotics)	3,99 (87%)	0,55 (12%)	0,05 (1%)	4,59	2,48 (28%)	5,22 (59%)	1,15 (13%)	8,85

litter was thus not accumulating on the river bed. At station B, however, the annual mean standing stock in the river was roughly double the total annual litter fall, indicating an accumulation of allochthonous detritus on the river bed. Table 3 shows that stem litter and acorns, but not soft litter, were accumulating in the system. This point is dealt with in the Discussion, but the subsequent investigations focused on the soft litter, which was the major contributor to litter fall.

All soft litter-fall at station A was from indigenous, evergreen trees (Fig. 2). The leaves, flowers and fruit were easily identifiable, with only a small fraction (3%) being unrecognisable frass. *Brabejum stellatifolium*, the wild almond, and *Metrosideros angustifolia*, the lance-leaf myrtle, both endemic to the area, were the main contributors of litter. Proportions shifted on the river bed, with an expected increase in unidentifiable detritus (3% to 19%). Most species decreased in proportion because of this, though *Cunonia capensis*, the red elm, and *Olinea cymosa*, the hard pear, showed an increase. As no *O. cymosa* and only one small *C. capensis* were present at station A, leaves of these species, and presumably all others, must have been imported from upstream. The ratio of *Brabejum stellatifolium* to *Metrosideros angustifolia* was much the same on the river bed as in litter traps, suggesting leaves of the two species were disappearing from the system at the same rate.

All soft litter at station B was from exotic trees (Fig. 2). The main contributors were *Populus canescens*, the grey poplar, and *Quercus*

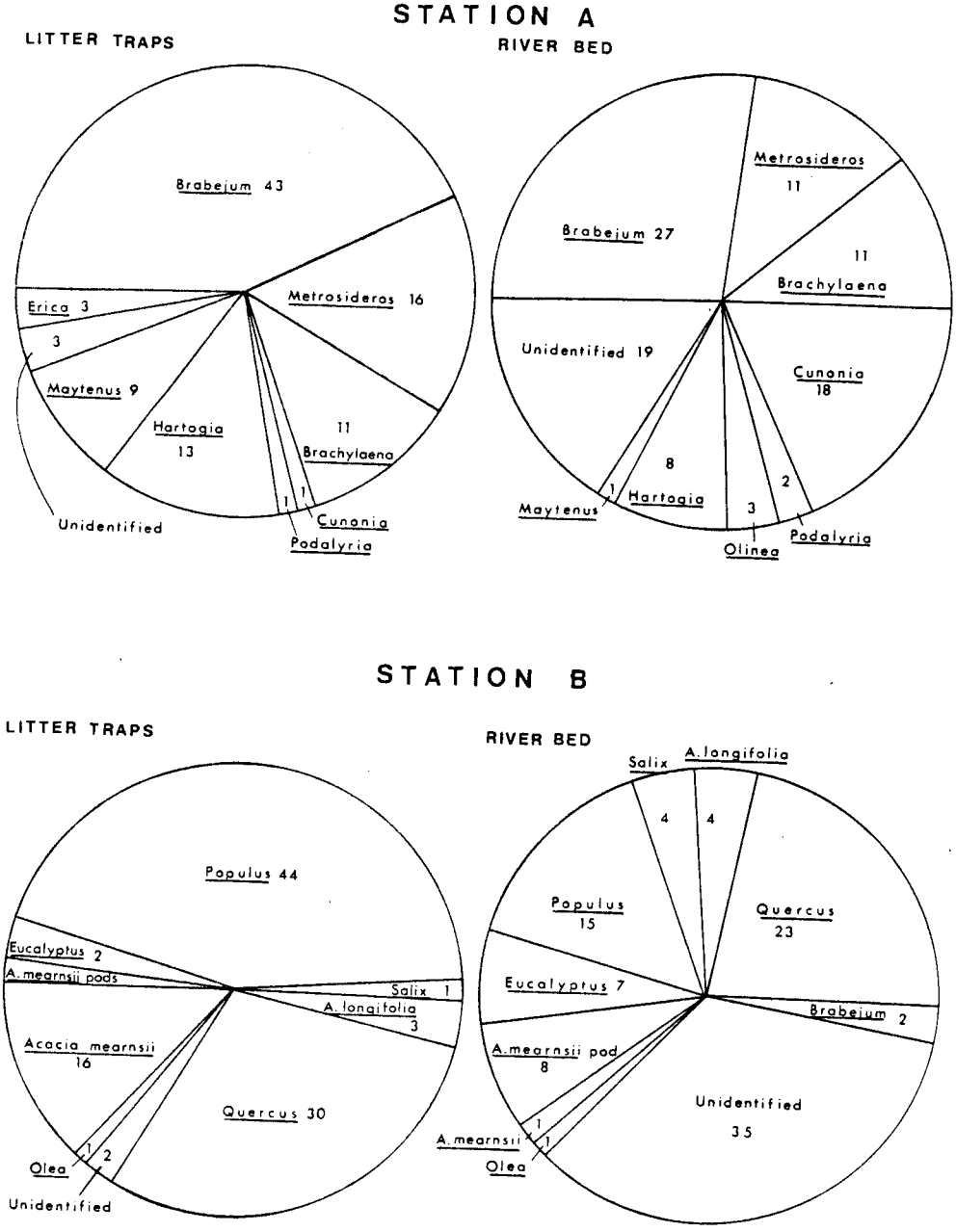

Fig. 2 Percentage dry mass composition of soft litter over one year, in litter traps and on the river bed, at the two stations. Full species names:

station A: *Brabejum stellatifolium, Metrosideros angustifolia, Brachylaena neriifolia, Cunonia capensis, Podalyria calyptrata, Hartogia schinoides, Maytenus oleoides, Erica caffra, Olinea cymosa.*

Station B: *Populus canescens, Quercus robur, Salix babylonica, Acacia mearnsii, Acacia longifolia, Olea africana, Eucalyptus* sp.

robur, the pedunculate oak, both deciduous, followed by the evergreen black wattle, *Acacia mearnsii*. The amount of unidentifiable frass was low in the litter traps, but considerably higher on the river bed (35%). Deciduous leaves, such as *Populus* and *Quercus* decreased proportionally from litter trap to river bed, while tougher material (*Acacia* pods, *Eucalyptus* leaves) became more obvious. The shift in the ratio of *Quercus* to *Populus*, between litter traps and river bed, suggests that *Populus* was disappearing from the system faster than *Quercus*. Tough leaves of *Brabejum*, alone of the upstream fynbos species, were reaching station B in recognisable form.

Data from the litter-trap and river-bed samples were used to ascertain monthly fluctuations in the biomass of soft litter (Figs 3-6). There was only one peak of litter-fall per year at station A (Fig. 3a), which occurred in mid-summer. Litter-fall was rare in winter, but rose sharply in late spring to a peak in December. The level then gradually fell again through the autumn, to return to the low winter value. This pattern was reflected on the river bed (Fig. 3b), where leaf packs were rare through the winter. Percentages of identifiable material were always high in litter traps (Fig. 3a), but somewhat lower on the river bed while following no obvious trend (Fig. 3b). The two main contributors of soft litter, *Brabejum* and *Metrosideros*, displayed the pattern of leaf-fall described above, and both flowered in summer at roughly the same time as leaf-fall (Fig. 4). The phenomena of summer leaf-fall and flowering are common among fynbos species.

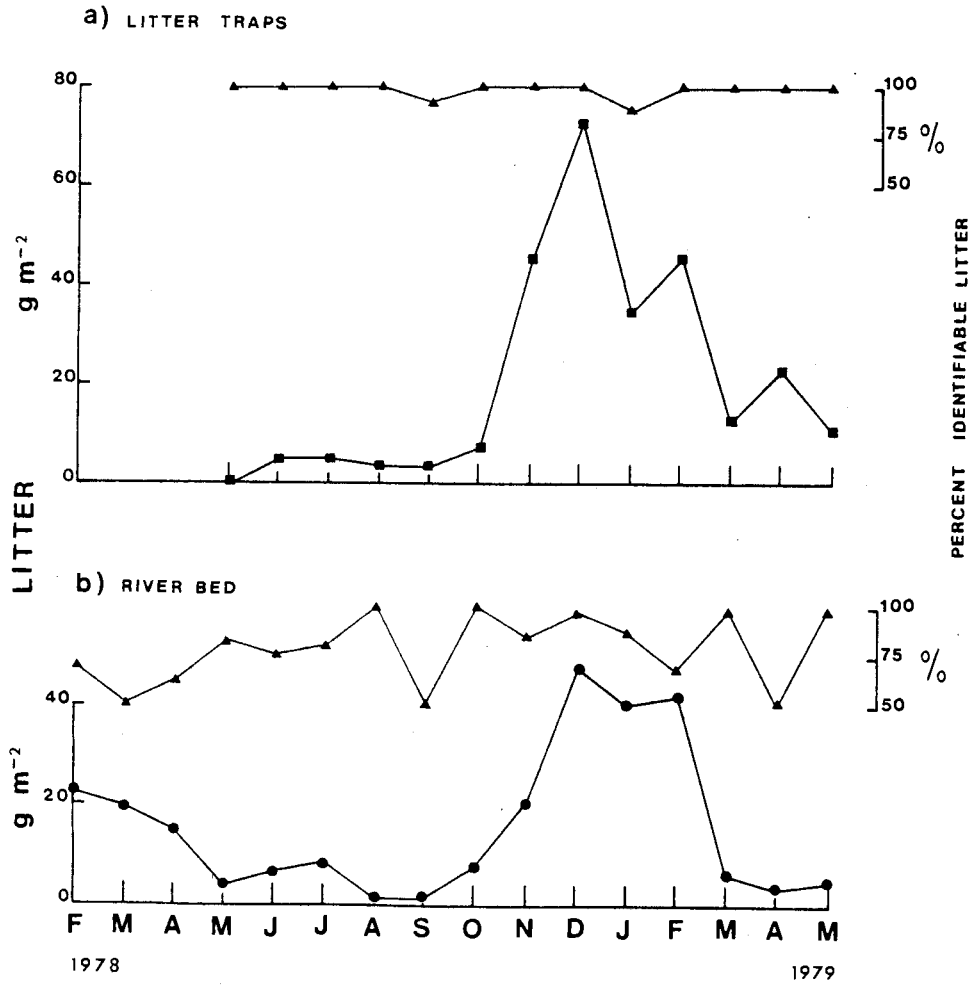

Fig. 3 Station A: monthly fluctuations in percentage of identifiable litter (▲), and in total dry mass of soft litter (leaves, flowers, fruit) in litter traps (■) and on the river bed (●).

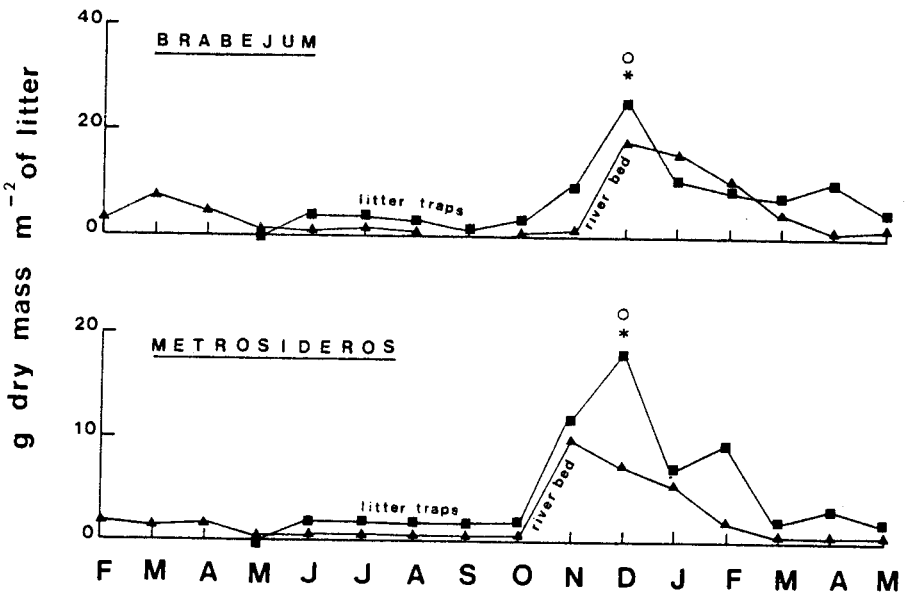

Fig. 4 Station A: monthly fluctuations in the dry mass of soft litter in litter traps (■) and on the river bed (▲) of the two main contributing tree species, *Brabejum stellatifolium* and *Metrosideros angustifolia*
* = flowering time; O = leaf-fall.

Two peaks of litter-fall occurred at station B during the year (Fig. 5a). A very high autumn peak, caused by deciduous leaf-fall, and a smaller spring peak from blossoms, were separated by periods of sparse litter-fall, with the lowest values being in late winter. This pattern was reflected on the river bed (Fig. 5b), but lagged about one month behind peaks in the litter traps. The two main contributors of soft litter, *Populus* and *Quercus*, followed the same pattern of leaf-fall (Fig. 6), though their spring blossoms (which were of considerable bulk in the case of *Populus*) had little impact on the amount of detritus on the river bed. Possibly the fluffy *Populus* catkins were washed from the area before they could sink, since station B was just below the upstream extremity of the *Populus* belt. At times both species, unlike those at station A, had slightly higher levels of litter on the river-bed than was falling from the trees, suggesting that there was an additional source of allochthonous detritus, possibly blow-in or drift. Other deciduous species at station B (e.g. *Salix babylonica*) exhibited the spring blossom autumn leaf-fall pattern, while evergreen exotics there (*Acacia mearnsii*, *Acacia longifolia*, *Eucalyptus* sp.), like their indigenous counterparts at station A, displayed a summer leaf-fall.

At station B, percentages of identifiable material were always high in litter traps (Fig. 5a), but considerabby lower on the river bed (Fig. 5b). Lowest levels of identifiable material on the river-bed were in early spring, when deciduous leaves had been decaying all winter, and before the spring fall of blossoms. Field observations showed that though new leaves of several deciduous species were

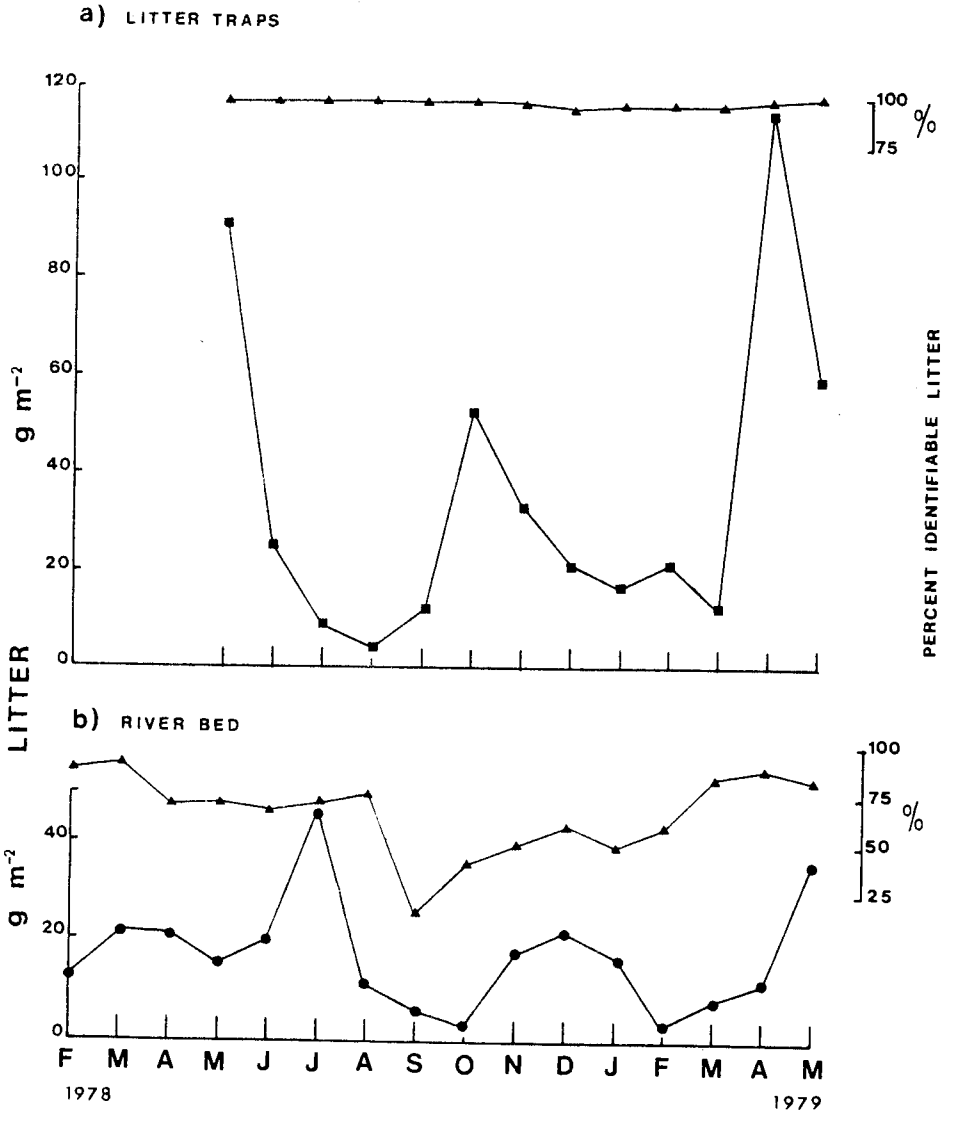

Fig. 5 Station B: monthly fluctuations in the percentage of identifiable litter (▲), and in total dry mass of soft litter in litter traps (■) and on the river bed (●).

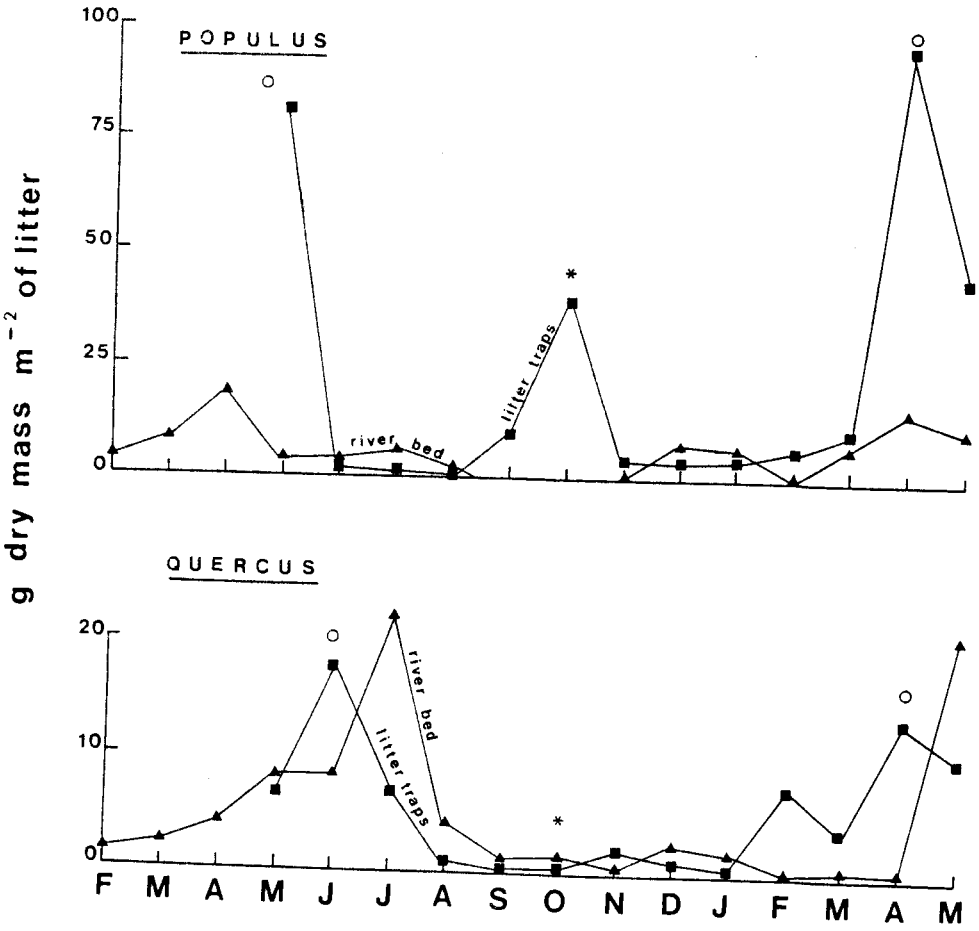

Fig. 6 Station B: monthly fluctuations in the dry mass of soft litter in litter traps (■) and on the river bed (▲) of the two main contributing species, *Populus canescens* and *Quercus robur*. * = flowering time; O = leaf-fall.

abundant on the river bed in autumn, by mid-winter differential decay had occurred, with leaves of some species (e.g. *Quercus, Salix*) still relatively intact, while those of other species (e.g. *Populus*) were barely recognisable.

The mean contribution of the four main species to the soft litter (in g dry mass m^{-2} $month^{-1}$), averaged over a year, were: *Brabejum* 7,21, *Metrosideros* 4,33, *Populus* 21,45, *Quercus* 5,22.

The potential of leaves of the four species to lose soluble substances on emersion in water was investigated in the leaching experiment. Twelve hours after submersion of the leaves in the jars of water, noticeable colouring of the water occurred in jars containing *Populus* leaves, and by 24 h the water in all jars was coloured, but least so in those containing *Quercus*. After 4 - 5 days, colouring of newly-added water decreased, and 1 - 2 days later transparent floating masses of micro-organisms appeared, attached to the leaves. These were most obvious in jars of *Metrosideros* and least so in jars of *Brabejum*. After three weeks, water in jars of *Quercus* and *Populus* smelt strongly, as did that in the remaining jars one week later, and by then a thick oily scum covered the surface of the water in jars of *Populus*. The accumulations of micro-organisms, the scum and the smell began to disappear in the fifth week, and by the eighth week the water in all jars was colourless and odourless. Few further changes were observed: the leaves remained intact to the end of the experiment (17 weeks), though by 12 weeks tiny particles of leaves were floating in all jars.

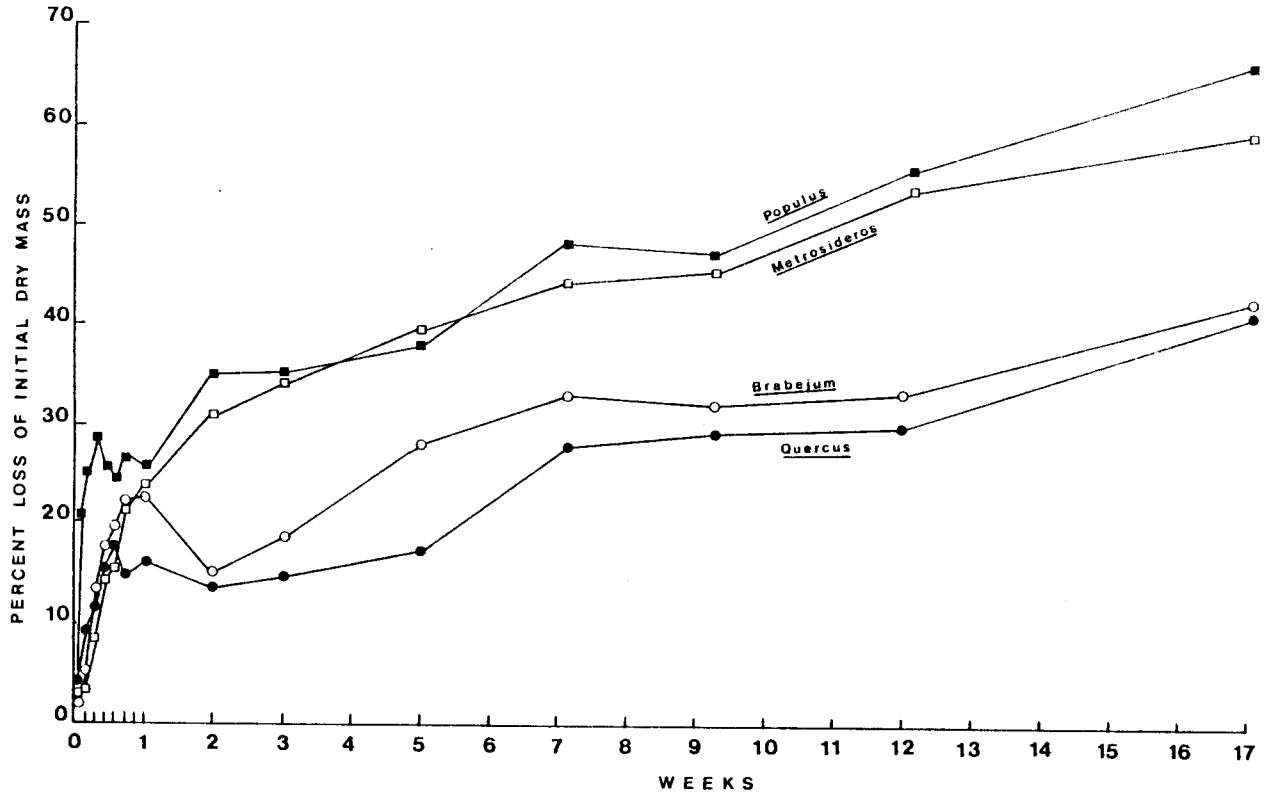

Fig. 7 Loss of mass of leaves of the four experimental species, due to leaching. Open symbols - evergreen fynbos species. Closed symbols - deciduous exotic species.

Measurement of weight losses revealed that leaching was rapid in the first 2 - 4 days (Fig. 7). By the end of one week *Populus* showed the greatest weight loss (26% of its initial dry mass), and *Quercus* showed the least (16%). The rate of leaching then slowed down, with *Populus* and *Metrosideros* showing a similar higher rate of loss and *Brabejum* and *Quercus* showing a lower rate of loss. The trend continued to the end of the experiment (17 weeks), by which time *Metrosideros* had lost 59% of its initial dry mass, *Populus* 66%, *Brabejum* 43% and *Quercus* 41%.

Data from bags of leaves submerged in Window Stream were used to determine the loss of weight of submerged leaves due to fragmentation, decay and the activities of detritivores. Losses above that already lost as leachate (Fig. 7) could be separated into the losses of fine particulate organic matter (FPOM < 0,5 mm) and of coarse particulate organic matter (CPOM 0,5 to 4,0 mm).

Weight losses from fine-mesh bags followed the same pattern as in the leaching experiment, with an high initial loss, followed by continued gradual loss throughout the rest of the experiment (Fig. 8). After 15 weeks the losses, compared to those resulting from leaching (which are given in brackets) were: *Metrosideros* 64% (57%), *Populus* 81% (62%), *Brabejum* 52% (39%), *Quercus* 51% (36%). Loss of FPOM was greatest from *Populus*, the leaves of which were very fragile from 7 weeks onwards. Leaves of the other species were more robust and *Quercus* in particular remained stiff and strong to the end. No obvious grazing by detritivores occurred on any leaves, though small

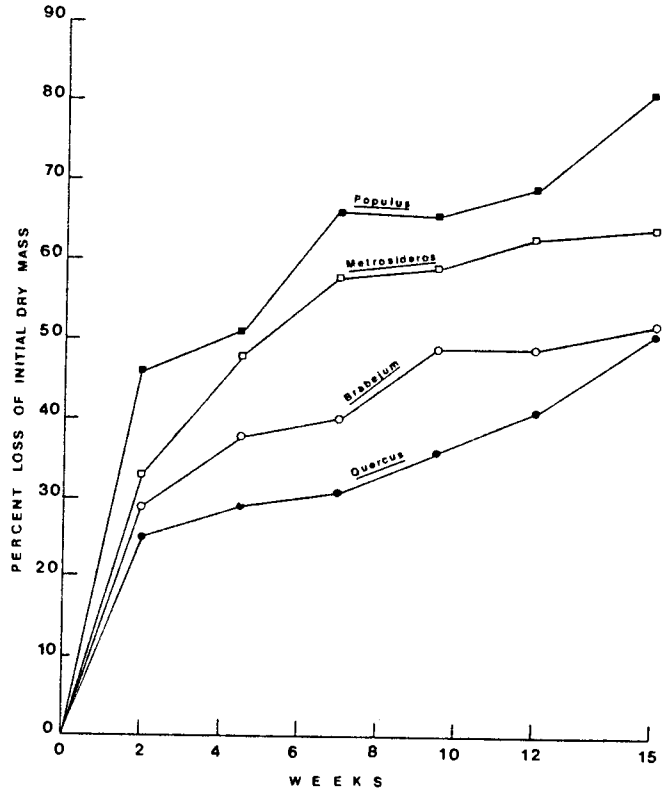

Fig. 8 Loss of mass of leaves of the four experimental species, when submerged in fine-mesh bags in Window Stream. Open symbols - evergreen fynbos species. Closed symbols - deciduous exotic species.

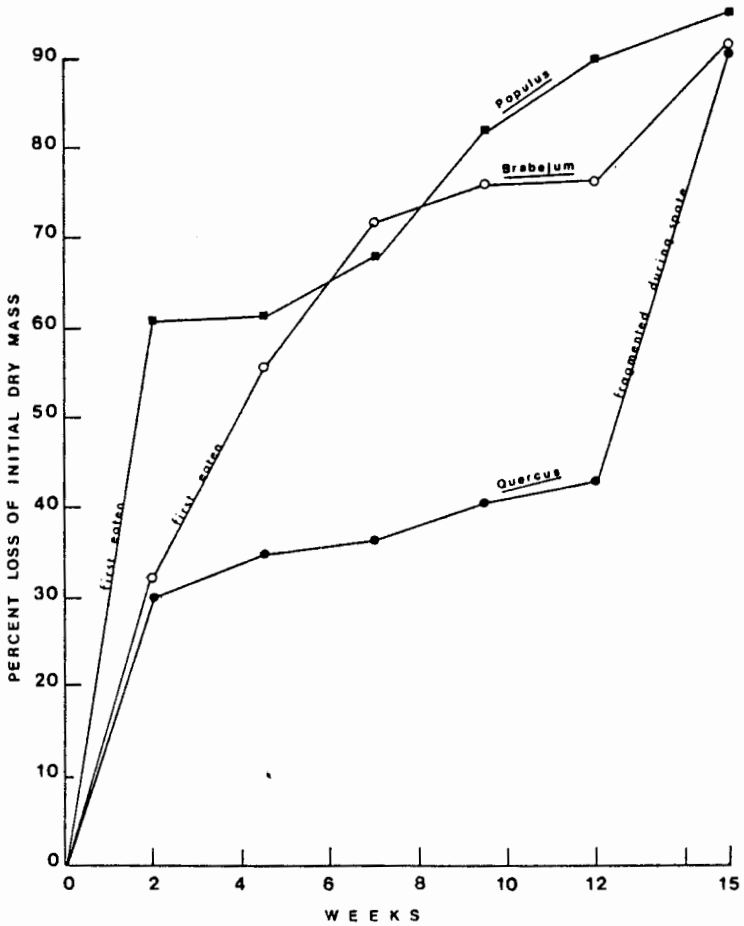

Fig. 9 Loss of mass of leaves of three of the four experimental species, when submerged in coarse-mesh bags in Window Stream. Open symbols - evergreen fynbos species. Closed symbols - deciduous exotic species. Losses from *Metrosideros* could not be measured accurately, as the slender leaves tended to slip through the coarse mesh of the bags.

invertebrates were found in the samples.

Weight losses from coarse-mesh bags were higher (Fig. 9) as a result of the leaves being eaten (*Populus*, *Brabejum*) or due to fragmentation (*Quercus*). *Populus* leaves were attacked by detritivores almost immediately, and lost 60% of their weight in two weeks. The tough leaves of *Brabejum* became virtually skeletonised next, while by that stage losses from *Populus* had decreased, so that by six weeks losses from both species were equal at 65%. Losses from *Populus* then increased again as the fragile leaves disintegrated, while the *Brabejum* curve flattened as feeding by detritivores tailed off. Accurate measurements of losses of CPOM from *Metrosideros* were not possible, as the slender leaves easily slipped through the large apertures of the bags. Bags of leaves were included in the samples, however, to ascertain the readiness with which *Metrosideros* was utilised by the aquatic fauna. Losses of CPOM from *Metrosideros* would probably be in the same range as those for *Brabejum* and *Populus* - leachate and FPOM were lost from *Metrosideros* at a rate intermediate of these two species (Figs 7 & 8), and skeletonisation of the leaves by detritivores in the coarse-mesh bags occurred as early as two weeks after submersion, so the leaves were obviously palatable. *Quercus* alone showed no attraction for detritivores (Fig. 9). After the initial leaching, loss of CPOM from *Quercus* was slow until 15 weeks, when extensive fragmentation occurred during a spate. Though the remaining leaves would then have been unrecognisable in a stream, they still showed little sign of having being eaten.

Table 4 shows the invertebrate species present in a single sample taken from the substratum of Window Stream, compared with those occurring in the submerged litter-bags during the experimental period. Most of the animals in the bags were small (5 mm or less in length), and occurred as often in fine-mesh bags as in coarse-mesh ones. As the leaves in the fine-mesh bags were not skeletonised, the 0,5 mm-wide apertures must have excluded the shredders that were present in the coarse-mesh bags. The species most likely to have been shredding the leaves is the largest present, the amphipod *Paramelita nigroculus*, which was never found in fine-mesh bags.

There were no trends in numbers or species of invertebrates in bags of different types of leaves - bags of *Quercus* contained animals as often as did those of the more palatable species. Nor were there obvious trends in the number of animals present in bags after different periods of submersion; numbers were high in bags collected at 2, 7 and 9,5 weeks, and were low in those collected at 4,5, 12 and 15 weeks. Lowest numbers were in samples collected within three days of a spate, and it is felt that the animals may shelter during periods of high discharge, probably by migrating down into the river bed.

4.2 GROWTH EXPERIMENTS

In winter several species that are abundant in the headwaters of the Eerste River (station A) extend down into the lower reaches (station B).

TABLE 4 Invertebrates present in Window Stream during the winter 1982.

SPECIES	ON SUBSTRATUM (June)	IN LITTER BAGS	
		Fine-mesh bags	Coarse-mesh bags
OLIGOCHAETA	-	**	**
AMPHIPODA			
Paramelita nigroculus	***	-	**
EPHEMEROPTERA			
Castanophlebia calida	**	*	*
Lestagella penicillata	**	-	*
PLECOPTERA			
Aphanicerca spp	***	**	***
TRICHOPTERA			
Athripsodes spp	-	*	***
COLEOPTERA			
Epidelmis capensis	*	*	*
Helodidae Larva	*	-	-
Ptilodactylidae Larva	*	*	*
Dryopidae Adult	-	*	*
? Noteridae Adult A	-	-	*
Adult B	-	-	*
Adult C	-	*	*
DIPTERA			
Simuliidae	*	*	*
Blephariceridae	*	-	-
Rhagionidae	*	*	*

Key: *** abundant ** common * present - absent.

Individuals of one such species, the detritivorous ephemeropteran *Castanophlebia calida* appear as very small nymphs as the winter rains begin, their univoltine life cycles lasting for five months at station B, but extending through nine to 12 months at station A (part 3). Nymphs of the shorter-lived downstream population grow faster and are considerably larger at emergence than those from the headwaters. The winter fauna as a whole displays a similar pattern, animals in the lower reaches completing their life cycles much more quickly than those in the mountain stream (King, 1981). The obvious downstream increase in the turnover of *C. calida* prompted the question of whether poorer quality and/or lower quantity of food at station A could be responsible for its slower growth there than at station B. As the lower reaches are enriched with treated sewage and agricultural run-off, and are warmer, the high rate of turnover of *C. calida* there need not necessarily be linked directly to the higher input of energy from riparian trees. It was felt, however, that investigations of the growth of this species at the two stations might reveal factors inherent in the fynbos vegetation which could cause lower production in streams that receive predominantly fynbos litter.

Castanophlebia calida is an ideal experimental species, as it is abundant throughout the western Cape, its nymphs can be distinguished from other species and their sex determined at an early stage, and its univoltine life cycle ensures that growth patterns are easy to interpret.

An analysis of the gut contents of 12 *C. calida* nymphs revealed no

green or blue-green algae, other than several different diatoms which are typical of fresh waters. Staining of the gut contents revealed no starch grains, indicating that fresh leaves were not being eaten. Pine pollen was present (there are pine plantations near the river) as were angiosperm cells such as stone cells, moss rhizoids and long, tough, fibrous cells typically found in twigs of fynbos species. At least 50% of the material appeared to be a fungal and/or bacterial film. This contained much unidentifiable material, some of which may have been leaf cuticle (i.e. from a leaf in the first stages of decay). According to the trophic relationships defined by Cummins *et al.* (1973) and Cummins (1974), the nymphs are fine-particle feeders, or gathering-collectors. When feeding, the maxillae move out sideways with the maxillary palps extended and then sweep inwards, gathering the decaying, woolly layer from the surface of a dead leaf. The maxillae then move together under the head and the gathered material is transferred to the mouth.

In a preliminary laboratory experiment, the nymphs survived for 15 days in a tank that contained stones and river water, but no leaves or other food. In another experiment, however, where the sides of the tank and the stones were scrubbed clean of slime each day, the nymphs died within three days. The animals thus appear to be able to survive, at least for limited periods, on the microbes which form a film on submerged surfaces. The microbes in the tank, in turn, must have received their nutrients from the river water. In the river, the nymphs may thus survive times when allochthonous detritus is scarce by exploiting such microbial films on stones of the river bed.

An initial feeding experiment was undertaken to discover if different growth patterns resulted when nymphs were kept at two different temperatures (representing the mean winter temperatures of the water at stations A and B), and provided with a food source consisting of leaves from either fynbos or exotic, deciduous species. Data from this and earlier work on *C. calida* revealed that the female nymphs are significantly greater in size than the male nymphs (t test $p < 0,05$) during all but the earliest part of their lives. Female nymphs are also significantly more common than males (chi square: $p < 0,01$) and, during experiments at least, the rate of mortality of males was significantly higher than that of females (chi square: $p < 0,02$). Growth data for males and females were therefore analysed separately; those for the females are presented here since data for the male nymphs showed the same trends.

The mean growth of female nymphs during the experiment is shown in Table 5. The highest growth rate was in the fynbos tanks held at the lowest temperatures, but an analysis of variance of the data (Table 6) revealed that the effects of the treatments were not significantly greater (at the 0,05% level) than the residual variance due to random error. The animals apparently had sufficient food for differences in food quality and water temperature not to be critical to growth. Animals in the tanks containing leaves of exotic species fared less well than those in tanks of fynbos, however, as mortality in fynbos tanks averaged 9% as opposed to 55% in tanks of exotic leaves. Losses of weight by the leaves during the experiment (eight weeks) were 29 - 30% from fynbos, and 48 - 60% from

TABLE 5 Mean growth (mm) of female nymphs of *C. calida* during the first feeding experiment.

Replicate Number	10°C Fynbos	10°C Exotic	15°C Fynbos	15°C Exotic
1	1,95	2,05	2,12	1,50
2	2,61	1,71	1,60	1,86
3	2,13	1,66	1,71	2,17
Grand mean	2,23	1,81	1,81	1,84

TABLE 6 Analysis of variance of data from Table 5

Source of variance	Sum of squares	Degrees of freedom	Mean squares
Between treatments	0,38	3	0,127
Residual	0,69	8	0.086
Total	1,07	11	

$$F = \frac{0,127}{0,086} = 1,477 \qquad p > 0,05$$

exotic species. Since these losses are similar to those described above for leaching alone, it seems likely that *C. calida* was not eating the leaves themselves. Nymphs of *C. calida* which were collected from the river at the beginning and end of the experiment, showed that growth in the river had been much slower than in the tanks - a mean of 0,4 mm in the river as opposed to between 1,5 mm and 2,6 mm in tanks.

A second experiment was undertaken to discover if different growth rates resulted when nymphs were provided with different quantities of leaves as their food source. For both male and female nymphs total growth varied in a manner relating to food supply (Fig. 10). Nymphs grew least in tanks with the lowest mass of leaves, and growth increased to a maximum then declined slowly with increases in the mass of leaves. At high levels of food availability growth was thus somewhat lower than in tanks in the middle of the food range. The point of suppressed growth was reached at a lower level of food supply in tanks of exotic leaves than in fynbos tanks. Thus, growth appeared to be suppressed if more than 1 g of leaves of exotic species was present, while it continued to increase in tanks of fynbos until about the 3 g level. In tanks containing the highest amount of exotic leaves, high mortality accompanied suppression of growth, particularly in the case of male nymphs (Fig. 10). At the lower levels of food supply (1 g and below), growth was greatest in tanks containing exotic leaves while at the higher end of the food range, growth was greatest in fynbos tanks.

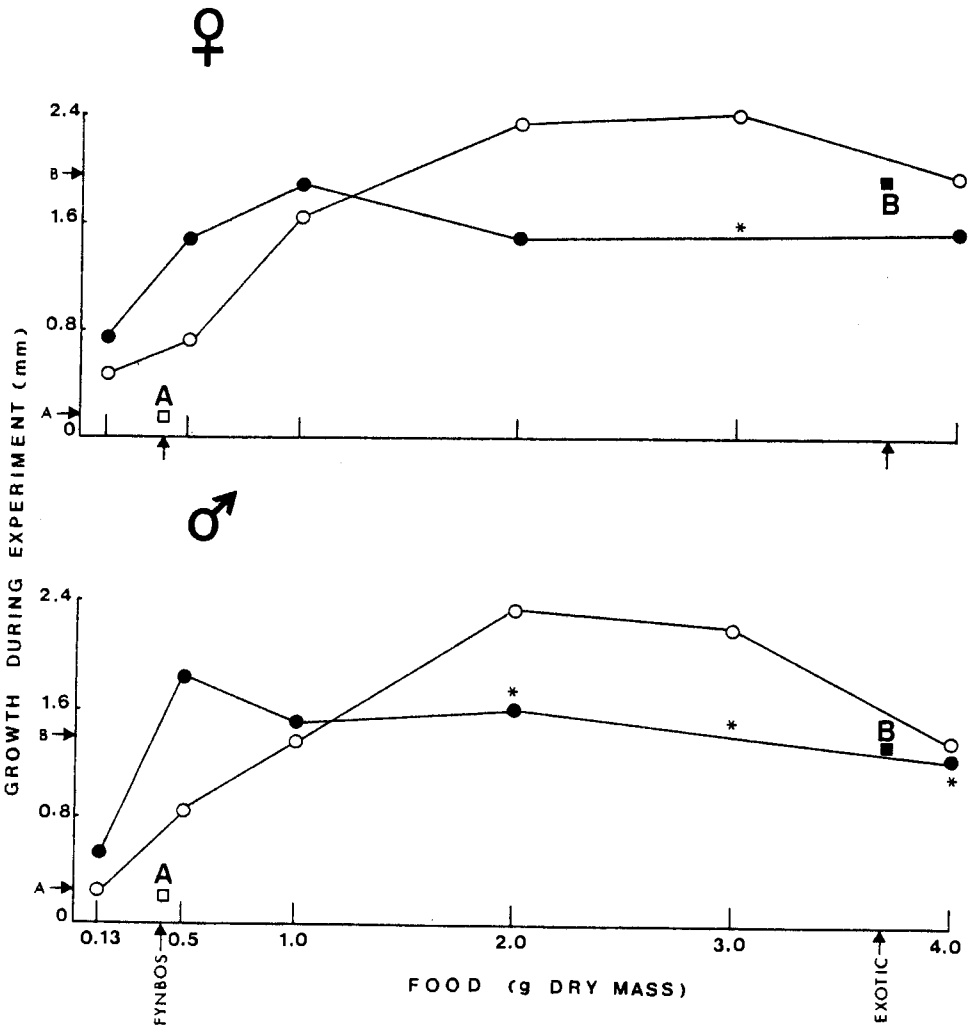

Fig. 10 Growth of nymphs of *Castanophlebia calida* fed different amounts of food. Diet: O leaves of fynbos species; ● leaves of deciduous exotic species; * = mortality rate more than 50%. Arrows on the Y axes show growth of nymphs of *C. calida* in the river at stations A and B, during the same period in which the experiment was conducted. Arrows on the X axes indicate the maximum amount of allochthonous detritus from fynbos or exotic species available to 20 nymphs in the river, as calculated in the Methods. Points A and B thus show the growth attained by the nymphs at stations A and B in the river respectively, at the maximum food levels theoretically available to them.

Figure 10 indicates the growth of nymphs of *C. calida* at stations A and B (i.e. in the river), during the same period in which the experiment was conducted (Part 3), at the maximum food levels theoretically available to them. For both sexes, growth in the river was less at station A than in the tanks of fynbos, but greater at station B than in the tanks of exotic leaves.

5. DISCUSSION

A comprehensive body of literature has appeared in the last two decades, which deals with the functioning of stream ecosystems, and particularly with the dependence of low order streams on energy received from outside the system (Cummins *et al.*, 1966). Such heterotrophy appears to decrease downstream, with the streams becoming increasingly autotrophic, though Minshall (1978) points out that even headwaters of unshaded streams in semi-arid regions may be primarily autotrophic.

The fate of allochthonous detritus in streams, mainly in the form of litter-fall from riparian trees, is now well understood. Briefly, leaves falling into a stream rapidly leach out dissolved organic substances, up to one quarter of their dried mass in a process that is largely temperature-independent (Petersen & Cummins, 1974). During the conditioning period colonisation of the leaves, principally by fungi, then occurs (Kaushik & Hynes, 1971), in a sequence that coincides with the leaching rate of the leaf species: fast-leaching species are colonised first (Hynes, 1963). The leaves, or more probably the microbes on the leaves, then attract detritivores, but the macro-invertebrates eventually turn from the leaves as the density of microbes decreases with exhaustion of the softer leaf parts (the post-conditioning period) (Cummins *et al.*, 1973; Boling *et al.*, 1974; Cummins 1974). Physical abrasion and non-feeding

activities of the fauna further disintegrate the leaves, and particles of all sizes may be washed away in the current. Most leaves disappear or disintegrate to unrecognisable fragments within a year of falling in the water (De la Cruz & Post, 1977; Petersen & Cummins, 1974). Post-leaching decomposition of the leaves (i.e. microbial activity) increases with increase in temperature and with increase in nutrient content of the water (Kaushik & Hynes, 1968; Short & Ward, 1980). Fractions of litter which are more resistant to decay (wood, bark) form a reserve pool of food (Anderson *et al.*, 1978) which, together with the leaves, flowers etc., result in a 'processing continuum' (Petersen & Cummins, 1974) of different material continually becoming available to detritivores.

In this study, the dynamics of allochthonous detritus in two stretches of a western Cape river have been investigated, to increase our understanding of the influence of the indigenous fynbos vegetation on streams that run through the fynbos biome. The mountain stream zone of the Eerste River (represented by station A) flows through mature, undisturbed mountain fynbos, and is thought to be heterotrophic because of the shading effect of riparian trees and the scarcity of aquatic macrophytes. The enriched lower reaches (represented by station B), where semi-submerged green plants are abundant along the banks, probably tend toward autotrophy.

I have particularly considered the quantity of allochthonous detritus entering the river at the two stations, and its nature; the speed at which detritus from fynbos vegetation decays in comparison with

that from exotic species; whether the leaves of fynbos species are palatable to aquatic detritivores, and what growth the animals show on such a diet; how the fall of litter into the river is related to the known seasonal cycles of the riverine invertebrate fauna; and whether the low secondary productivity of mountain streams of the fynbos biome can be explained by any of the above considerations.

5.1 THE ALLOCHTHONOUS DETRITUS

Total litter-fall from riparian trees along the Eerste River was considerably higher at station B than at station A (Table 3). The amount at station B was similar to total litter production of warm, temperate forests between latitudes 30° and 40° (Bray & Gorham, 1964; Blackburn & Petr, 1979; Versfeld, 1981), and to the amounts of allochthonous detritus entering streams in other countries (Petersen & Cummins, 1974; De la Cruz & Post, 1977). Litter fall at station A, however, was closer to values for cool temperate forests of the northern hemisphere at latitudes of about 50°. In reality, the vegetation at station A more closely resembles a shrub community than a forest, being described by Kruger (1979) as 'broad sclerophyllous closed-shrub... (that) form(s) a continuous canopy about 5 - 6 m high, with sparse understories of lower shrubs and ferns'. Litter production from this riparian community lies within the range 0,9 - 4,9 t ha^{-1} yr^{-1}, given for litter production of mediterannean ecosystems (Day, in press).

The amount of litter falling into the river is assumed to be similar to that falling into the litter traps, because of the closed canopy over much of the river. The relative importance of two additional sources of litter - drift from upstream and blow-in from the banks - remains unknown, but fluctuations in the amount of litter in traps and on the river bed were so closely related in this study, that it has been assumed that data from the litter-trap samples adequately indicate the quality and quantity of litter reaching the river bed.

World-wide, wood and bark (stem litter) respectively produce an average 12 - 15% and 1 - 14% of this litter-fall (Bray & Gorham, 1964), while these elements, combined with flowers, fruit and other plant fragments produce 30% of the total, the rest being leaves. Stem litter at station B agreed with these figures (Table 3), while that at station A was considerably lower. It is difficult to obtain an accurate mean measure of stem litter over a small area, where its fall may be erratic, and a litter-trap is liable to catch 'all or nothing'. The low figure may therefore be due to sampling difficulties, but it is likely that these tough, small trees shed little bark and lose little wood.

The change in the proportion of stem and leaf litter between litter traps and the river bed indicates that wood and bark persist longer in the river than do leaves (Table 3). This is most obvious at station B, where stem litter and acorns together increased from 13% of total biomass of litter in traps, to 72% of that on the river bed. This tough fraction of the litter apparently persists for more than

one year on the river bed, for wood and bark were found in greater quantities there than fell in one year into traps. Again, the erratic fall of stem litter may have led to misleading results, but possibly such litter does accumulate on the river bed, to be swept away eventually by winter spates. The series of relatively dry winters that occurred before and during this study may have resulted in flow in the lower reaches being insufficient to scour the river bed free of woody debris. If this is so, harnessing of winter spates by the newly-completed dam on the river's headwaters could cause an additional and unforeseen change in the ecology of its lower reaches, if woody debris builds up on the substratum.

The mixed exotics at station B annually produce almost twice the biomass of soft litter than does the upstream indigenous vegetation (Table 3). Additionally, at station B, the temporal separation of blossoming and leaf-fall in the deciduous species (Fig. 6), together with the varied times of leaf-fall in the mixed evergreen and deciduous trees, results in a more continual introduction of allochthonous detritus into the river (Fig. 5) than can occur at station A, where the blossoms and leaves of fynbos both fall in summer (Figs 3 & 4).

Rates of leaching from the two fynbos species are within the same range as rates from the deciduous exotics (Fig. 7), and are similar to those reported from other countries. In Australia, Blackburn & Petr (1979) found that weight loss of *Quercus ?robur* increased from 12% to 22% of initial dry weight between 24 h and 8 weeks (9-26% in

this study), while from Canada, Kaushik & Hynes (1971), and from U.S.A., Petersen & Cummins (1974), both report a slightly lower rate of loss from *Q. alba* (about 5% after 24 h). Petersen & Cummins also give a 24 h loss of 19,2% of initial weight for *Populus tremuloides*, while in this study *P. canescens* lost 24,5% in the same period. Blackburn & Petr (1979) give figures for many other species, while Lock & Hynes (1975), McDowell & Fisher (1976) and Lush & Hynes (1978a and b) discuss the fate of this leachate in streams. The results here do not agree with Lush's finding (1972, quoted in Lock & Hynes, 1975) that deciduous leaves release more leachate per unit weight than do evergreens.

The subsequent loss of coarse and fine particles from the leaves, together with records of field observations, revealed the pattern of decay likely to have occurred in the Eerste River (Figs 7, 8 & 9). *Populus* leached fastest and presumably was colonised by microbes first, as it had been largely skeletonised by detritivores after two weeks submersion (Plate 3). After this feeding activity switched to *Brabejum*, and the rate of weight loss from *Populus* declined during its post-conditioning period. Seven weeks after submersion losses from *Brabejum* decreased, by which time many of the leaves had been largely skeletonised (Plate 4). Losses from *Populus* meanwhile had increased again with disintegration of the leaves, so both species were effectively unrecognisable after eight to 12 weeks submersion (Plate 5), and had virtually disappeared by 15 weeks. *Metrosideros* appeared to follow the same pattern of decay as it was readily eaten (Plate 6), but the tiny leaves may have been swept rapidly from the

Plate 3. The appearance of leaves from litter bags after two weeks submersion in Window Stream. Top row - fine-mesh bags. Left to right: Metrosideros, Brabejum, Quercus, Populus. Bottom row - coarse-mesh bags. Left to right: Brabejum, Quercus, Populus. Leaves of Metrosideros in coarse-mesh bags were not measured for weight loss and were not processed with the rest of the samples, and thus this species is missing from the bottom row. Leaves from the fine-mesh bags (top row) were virtually intact, while Populus in coarse-mesh bags (bottom row) was already partially skeletonised.

Plate 4. Leaves from litter bags after seven weeks submersion in Window Stream. Top row - fine-mesh bags. Left to right: Metrosideros, Brabejum, Populus, Quercus. Bottom row - coarse-mesh bags. Left to right: Brabejum, Populus, Quercus. Metrosideros is missing for the reason given in Plate 3. Leaves from fine-mesh bags were virtually intact, while Brabejum and Populus in coarse-mesh bags were equally skeletonised.

Plate 5. Leaves from litter bags after 12 weeks submersion in Window Stream. Top row - fine-mesh bags. Left to right: Metrosideros, Brabejum, Populus, Quercus. Bottom row - coarse-mesh bags. Left to right: Brabejum, Populus, Quercus. Metrosideros is missing for the reason given in Plate 3. Note that only the mid-rib remains of one of the Brabejum leaves from the coarse-mesh bags, and that fragmentation of Quercus is becoming obvious.

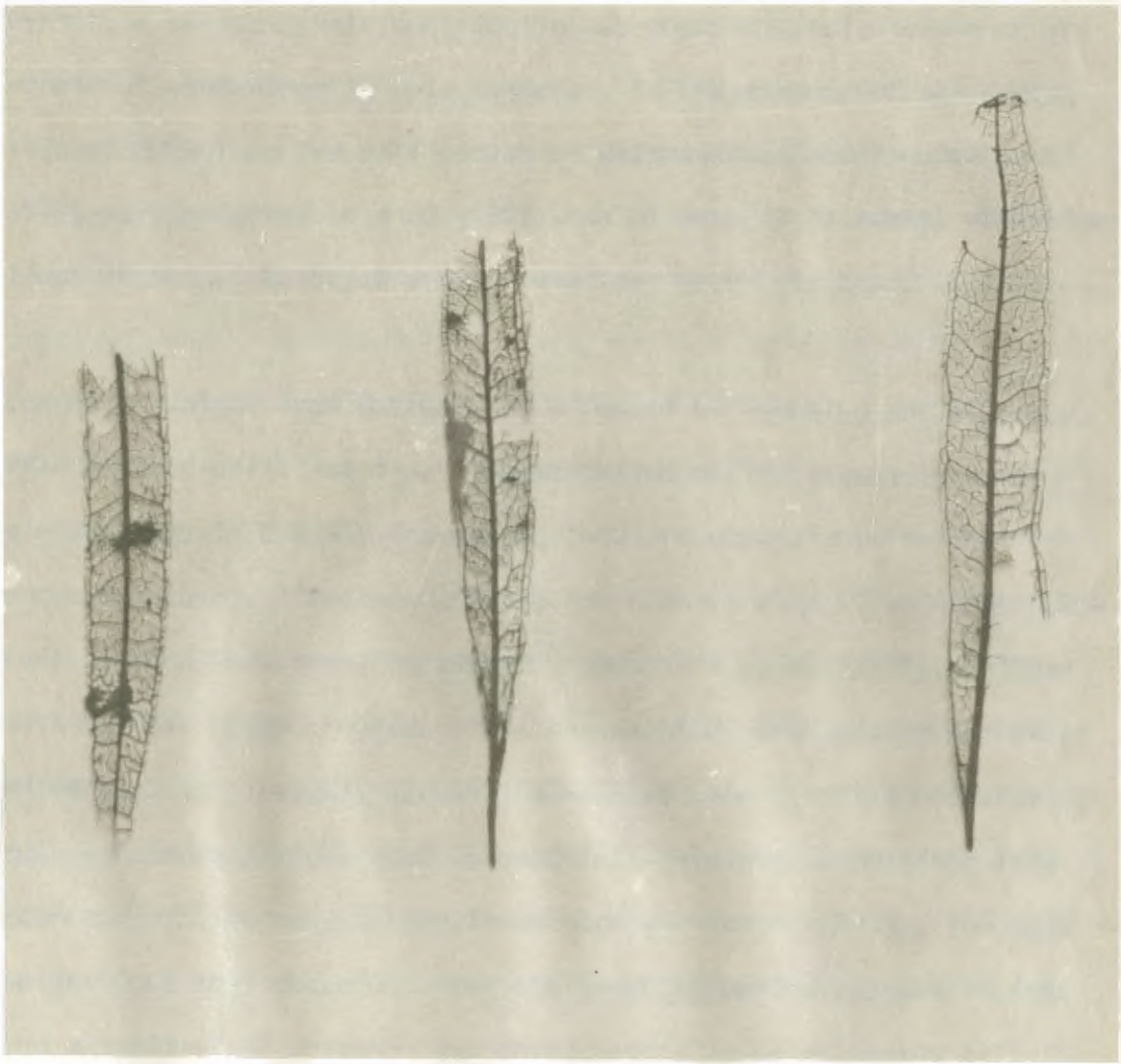

Plate 6. Close-up of leaves of Metrosideros after two weeks submersion in Window Stream. The isolated dark patches are all that remain of the fleshy part of the leaves.

system, limiting their contribution as food, at best, to one of an ephemeral appearance in late summer. In the absence of shredders, loss of FPOM from the soft leaves of *Metrosideros* and *Populus* would still have resulted in a 60 - 80% loss of mass in 15 weeks, while the tough leaves of *Brabejum* would have lost much less mass.

Losses of weight from *Quercus*, as a result of leaching and of decay, were similar until the final fragmentation of the leaves in late winter (Figs 7, 8 & 9), indicating they are unpalatable to detritivores (Plate 5). *Quercus* leaves are rich in lignin, and their slow rate of decay has been discussed by Kaushik & Hynes (1971). These authors have shown, however, that leaves of *Q. alba* are nevertheless eaten as a last resort, and in the western Cape *Q. robur* may provide such a reserve of food that is used in late winter when other food is scarce. In the case of the three more palatable species, the major weight loss that occurred after the leaching period was due to feeding activities of unidentified shredders. Isolated leaves arriving in the system during winter would likewise be skeletonised by them. The remaining, less-nutritious parts of the leaves would then be the major food base available to gathering-collectors such as *Castanophlebia calida*, and even this would disappear within four months of submersion.

Processing (or decay) coefficients, as proposed by Petersen & Cummins (1974), show that the rates of decay of *Populus* and *Metrosideros* are fast, while *Brabejum* is medium and *Quercus* borderline slow/medium. According to these rates, *Populus* and *Metrosideros* leaves falling into

a stream, would be unrecognisable in 3 - 4 months, *Brabejum* in 7 - 8 months and *Quercus* in 10 - 11 months. With detritivorous activity, some of these periods are considerably shorter (Fig. 9): most *Brabejum* and *Metrosideros* leaves falling into the stream in January (mid-summer), for instance, disappear by May (early winter), while *Populus* leaves falling in April, last only until early June. *Quercus*, also falling in April, remain uneaten through the winter, though escalating losses through fragmentation continually reduce the biomass of this food reserve. At station A, then, where the vegetation is characterised by a summer leaf-fall, to which *Brabejum* and *Metrosideros* are the major contributors, very little allochthonous detritus thus is available to detritivores during their winter and spring growth. In contrast, at station B, the widely different rates of decay of *Populus* and *Quercus* probably represent part of a continuum of available decaying material provided by the mixed riparian vegetation. The presence of greater amounts of this detritus on the river bed at station B at all times, compared with station A, appears to provide ample food for the detritivores during their winter growth.

5.2 THE GROWTH EXPERIMENTS

Temperature and food are recognised as two major parameters controlling growth of stream macro-invertebrates (Cummins, 1979), and understanding the interplay of these parameters in undisturbed

streams is of great importance if we are to predict biological responses to environmental change. Ward & Cummins (1979), after experiments with the stream detritivore *Paratendipes albimanus* (Chironomidae), concluded that temperature controls its seasonal growth and can prevent its development in winter, but that detrital food quality in the form of microbial biomass appeared to be equally important as a regulator of its growth. They pointed out that *P. albimanus* failed to grow at temperatures below 'its thermal limit' of 4°C, while 10°C was 'known to be favourable for growth'. Additionally, growth could be slowed or stopped by poor quality food, or accelerated by high quality food, and Ward and Cummins have suggested that the fine-particle detritus found in wooded headwaters (such as the one they studied) would permit relatively slow growth in the detritivores which fed upon it. This would be particularly true in the period immediately preceding the peak annual litter-fall, when microbial metabolism has removed all but the most refractory of material from the detritus.

In the present study, nymphs of *C. calida* held at 10°C or 15°C (typical winter temperatures of station A and B in the Eerste River) showed no significant differences in total growth, suggesting that growth of the species in the river should not be affected overly by the range of winter temperatures it is likely to experience. Food levels in the experiment were high, however, and significant differences in growth might have shown up if food had been scarce; this was not investigated.

On the other hand, the quality and quantity of leaves provided as food in the laboratory did affect the growth of *C. calida*. Nymphs fed different amounts of either fynbos or exotic leaves showed, up to a point, increased growth with increased food availability (Fig. 10). Above this point growth was less at the highest food levels than at moderate levels, and many animals in the tanks with exotic leaves died or responded sluggishly to stimuli. The point at which growth was maximal was reached at a lower food level in tanks of exotic leaves than in fynbos tanks, where mortalities were rare, suggesting that some factor associated with the exotic leaves was implicated in the mortalities. In addition, growth of the nymphs feeding on exotic leaves was less than at the equivalent station in the river, station B (Fig. 10), despite the presence of competing detritivores at station B, suggesting that some critical environmental condition met in the fast-flowing river was not met in the experimental tanks. If, for instance, the quality and/or quantity of leachate in the water of the tanks was implicated in the poor growth and high mortality, the survival of the species in the lower reaches of the Eerste River could be affected if adequate flow does not accompany the autumnal input of deciduous litter along these reaches.

The type of leaves offered the nymphs in the feeding experiment also became critical to growth at low food levels, for at the lowest food levels nymphs provided with leaves from exotic trees grew larger than did those provided with fynbos leaves. This suggests that if levels of allochthonous detritus at stations A and B were equal and low, nymphs at station A would still grow more slowly than

those at station B. The slower growth of nymphs of *C. calida* at station A in the river compared with that in tanks containing fynbos leaves (Fig. 10) suggests that among other factors, competition for food from other detritivores may have further reduced the food supply in the river, and thus reduced the growth of *C. calida*. Shredders, such as those that rapidly ate most of the experimental leaves placed in Window Stream, are known to constitute a larger proportion of the fauna in headwaters than in any other stretches of rivers (Cummins, 1979), and would be expected to eat a correspondingly large proportion of the detritus.

5.3 SUMMARY OF EVENTS IN THE RIVER

At station A young nymphs of *C. calida*, already partly grown, appear on the river bed in autumn, at about the same time as the first light rains occur (King, 1981). Conditions for their growth appear to be favourable then, with water temperatures not yet at the low winter levels, and with decaying leaves from the summer leaf-fall plentiful on the river bed. Growth of the young nymphs is rapid at this stage (part 3). When discharge increases and temperatures fall, most of the newly-fallen leaves will have been skeletonised, and all but the most refractory of material will have been removed from the remains by microbial activity (Ward & Cummins, 1979). In addition many leaves will have been washed from the system. Food will thus be scarce through winter and early spring (Fig. 3), and competed for

by a variety of detritivores, most of which, like *C. calida* will be half-way through their growth and needing ever-increasing amounts of food. At this stage, the selection of high-quality food is probably over-ridden by the scarcity of food in general, and gathering-collectors such as *C. calida* may exploit the microbial film on submerged rocks. Growth of *C. calida* virtually ceases during these months (part 3). In late spring, as discharge drops, temperatures climb and the input of litter increases (Fig. 3), *C. calida* starts to grow slowly again, until the summer emergence of small adults. Eggs laid in the river by the newly-emerged adults take slightly more than one month to hatch (own unpublished data), and the tiny nymphs presumably start their life cycle deep in the river bed as they do not appear on the surface of the substratum until autumn.

At station B the accumulation of pollutants during the summer months of poor flow (King, 1981), combined with the leaching of soluble substances from the massive input of autumn leaves, must result in water that is highly unsuitable for an aquatic species typically found in cold, fast-flowing streams. The mortalities of *C. calida* in tanks containing exotic leaves additionally suggests that the species is susceptible to higher levels of dissolved organic material. Young nymphs of *C. calida* consequently appear later at station B than at station A (own observations during years of poor rainfall), and possibly the autumnal increase in the river's discharge is more critical to their appearance there than in the upstream cleaner reaches.

Throughout the year more allochthonous detritus is present at station B than at A, and probably litter from different species continually arrives at a stage of decay where it becomes attractive to detritivores as food. The high nutrient content and higher temperature of the water presumably encourage greater microbial activity at station B, thus further boosting the supply. Growth of *C. calida* is fast from the nymphs' first appearance in late autumn, and pre-emergent nymphs which are much larger than those at station A are already present in early spring (part 3). Emergences are complete by mid-spring, and the species then disappears from these reaches for roughly six months.

5.4 *CASTANOPHLEBIA CALIDA* - TIMING OF LIFE CYCLE

Life cycles of *C. calida* at station A and B in the Eerste River fit into the categories given by Cummins (1974), in his general classification of stream macroconsumers. In this classification, the animals are categorised on the basis of their generation time, period of growth and method of feeding. At station A, *C. calida* has an annual life cycle starting in early autumn and including the following summer ('annual' category of Cummins), while at station B it has an annual life cycle that also starts in early autumn, but which is completed before the following summer ('annual-autumnal' category of Cummins). Thus this relict ephemeropteran, now restricted to the fynbos biome and to montane regions north to Natal

(Harrison, 1965), exhibits life cycle patterns that are widespread among stream animals in the Northern Hemisphere. Yet the theory that aquatic invertebrates have adjusted their life cycles to grow in winter, in order to take advantage of the autumn leaf-fall (Hynes, 1963; Petersen & Cummins, 1974; Boling *et al.*, 1975) cannot be applied to *C. calida*. At station A of the Eerste River the annual life cycle of this univoltine species (and of the aquatic community as a whole - King, 1981) commences in autumn, though the peak input of fresh allochthonous detritus occurs three months earlier, in summer. Detritus is thus scarce through most of its life cycle, and this is reflected in its growth pattern: rapid growth of new nymphs in autumn, followed by a pause or slowing of growth in winter, then increased growth again in late spring as the input of litter increases. The winter pause cannot be attributed to low temperatures as laboratory experiments have shown that the temperature of the water at station A in winter (10°C) is not sufficiently low to inhibit growth.

No such pause in growth occurs at station B, where detritus is more plentiful all year. Factors other than synchronisation with leaf-fall must be implicated in the life cycle of *C. calida* at station A, and these factors must outweigh the disadvantages of poor winter growth and low production. A likely factor is the avoidance of high summer temperatures by the early instars, as *C. calida* has cold stenothermic nymphs and, though it is widespread in the temperate western Cape it is confined to high altitudes in sub-tropical Natal (Harrison, 1965). Hynes (1970) points out that many varied devices

have been evolved by stream invertebrates to enable them to avoid unfavourable conditions and that in contrast to terrestrial habitats where low winter temperatures are unfavourable to many species, in streams the summer produces conditions that are avoided by a large proportion of the fauna.

Thus the low secondary productivity of mountain streams that run through the fynbos biome seems to be a result of low levels of food in the water. Terrestrial leaf litter is an important energy source for the streams and it disappears quickly on submersion, yet the invertebrates in the headwaters do not have life cycles that are synchronised to maximise on the peak input of this detritus. The resultant scarcity of food during most of their lives appears to be the cause of the very slow growth of the mountain-stream community.

6. SUMMARY

The mountain streams that run through the fynbos biome of the south-western Cape, South Africa, are characterised by low productivity. The sclerophyllous, evergreen fynbos vegetation through which the mountain stream section of the Eerste River runs produces about half the litter (2,67 t ha^{-1} yr^{-1}) that downstream deciduous trees do (4,59 t ha^{-1} yr^{-1}). In both areas the biomass and nature of the litter agree with data from similar vegetations in other countries. Peak litter fall from riparian fynbos in the mountain catchment is in summer, when leaves and blossoms fall at about the same time, while downstream, the deciduous trees display the more usual pattern of autumn leaf fall and spring blossoming. Leaves of the indigenous riparian trees in the fynbos biome leach and decay in water as quickly as do leaves from the deciduous exotics, and are as palatable to detritivores. Allochthonous detritus on the river bed thus disappears equally quickly from both stretches of river, but because of the lower input from fynbos, mean standing stock of detritus is lower in the mountain stream.

Turnover of a common riverine detritivore, the ephemeropteran *Castanophlebia calida* is much lower in the mountain stream than in the lower reaches, yet in a laboratory experiment no significant

differences in growth rate occurred when the animals were kept at different temperatures typical of the two stretches of river in winter (10°C and 15°C). The downstream increase in turnover of the species thus appears not to be due to the downstream increase in water temperature.

The nymphs also grew equally fast on a diet of fynbos leaves or deciduous leaves, provided the food was abundant, but when leaves were scarce nymphs on the fynbos diet grew more slowly. Thus if levels of allochthonous detritus at stations A and B were the same and low, nymphs at station A could be expected to show the least growth.

C. calida and the mountain-stream invertebrate community as a whole display annual, autumn-to-summer life cycles. Peak input of fynbos litter, which occurs in summer, is thus not fully exploited by the animals, as most of the litter has disappeared from the stream by late autumn. This is in contrast to downstream reaches, where *C. calida* appears at the same time as autumn leaf-fall, and where a variety of deciduous and evergreen trees occur. These trees provide a more continual input of litter than occurs at station A, and thus increase the likelihood that at station B some allochthonous detritus will always be at a state of decay suitable for detritivores. In the mountain stream *C. calida* grows slowly, with the emergence after 10 - 12 months of small adults, while in the lower reaches the nymphs grow faster and larger and take less than half that time to complete their development. The low productivity of the mountain-

stream population appears to be due to the scarcity of allochthonous detritus there during much of the animals' life cycles. Failure of the animals to synchronise their life cycles to coincide with peak inputs of food suggests that other factors are of more importance to their survival; avoidance of summer temperatures by early instars may be one such factor.

The experiments described above also revealed that when levels of detritus from exotic trees were high, growth of *C. calida* was suppressed and mortalities increased. As modification of the quality of the water by the leaves seemed to be implicated, the potential of the species to survive in the lower reaches of rivers such as the Eerste River might be adversely affected if adequate flow does not accompany the autumnal input of deciduous litter there.

ACKNOWLEDGEMENTS

My thanks to Professor Derek Mitchell and Dr Bryan Davies, and particularly to Professor George Branch, for criticising earlier drafts of this paper. Miss Judy Graves identified the gut contents of *Castanophlebia calida*, and Mr Parbhoo, cobbler, and Mr Joe Brilleman of Starpak made the litter bags for me. My thanks to the staff of Kirstenbosch Botanical Gardens for allowing me to work in Window Stream, and particularly to Mr McKenzie for his help in locating a suitable site and securing the litter bags in the stream. The South African Department of Forestry allowed me to work in the Jonkershoek Forestry Reserve, where station A was located.

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SUMMARY

SUMMARY

This study of the invertebrate fauna of a small south-western Cape river has revealed a logicality in the way such river systems function. The downstream changes in the quality of the river water and in the species and standing stock of the invertebrates of the Eerste River were clear, one-way changes, which resulted from a combination of climatic, geological, geographical, biological, physical and chemical influences. Different life-cycle patterns and growth rates of the invertebrates along the river indicated that the fauna could also adjust to downstream changes in their environment in additional ways, such as by growing faster and producing more generations in enriched parts of the system; and growth experiments with an ephemeropteran species revealed that the character of the riparian vegetation has a strong influence on the secondary production of the river's headwaters.

At the beginning of the study, faunal samples were collected monthly for 14 months along the length of the stony-bed reaches of the Eerste River (Part 1). Cluster analyses of the samples showed the presence of distinct groups of animals in the river, which were treated as separable animal communities. The communities on the stony bed were more clearly and restrictively distributed than those in the other major habitat, the marginal vegetation, and it was thought that the marginal vegetation is probably a more inhospitable and variable

habitat, especially in the headwaters where it is not present as continuous belts of vegetation along the margins of the water.

The distribution of the stony-bed communities clearly divided the study area into three longitudinal zones - the Mountain Stream, Upper River and Lower River - each of which coincided with an obvious physical zone and was characterised by a different chemical quality of water. While the Mountain Stream was unpolluted and relatively cool throughout the year (10 - 21°C), the Upper River was reasonably clean and slightly warmer (10 - 26°C) and the Lower River was markedly more polluted and warm (11 - 28°C). Conditions in the Lower River varied from poor in the summer to improved in winter when the discharge increased, but nutrient concentrations there were high throughout the year, mainly because of organic effluents from the town of Stellenbosch which was situated at the upstream extremity of the zone.

Temporal changes from one community to another were different in each zone. The Mountain Stream supported a year-long community (the winter mountain stream community - WMS) that consisted almost entirely of insects, and when these animals grew to maturity they were replaced by another identical community. There was a pause of variable length at the change-over time, when animals were scarce on the substratum of the Mountain Stream, but the reasons for the new community's later or earlier appearance in different autumns are not known. The Upper River supported alternating summer and winter communities (the summer

and winter upper river communities respectively - SUR & WUR), both of which were dominated by insects. The winter community occupied the habitat for roughly eight months of the year and was similar in species composition to the community in the Mountain Stream, which is why the year-long upstream community also has been called a winter community. Winter and summer communities, each lasting about six months, also occurred in the Lower River (the winter lower river community - WLR, and the transitional and summer lower river communities - TLR & SLR). While the species composition of the winter community in the Lower River was similar to those of the winter communities in the two higher zones, the main summer community of the Lower River (SLR) was quite different to that of the Upper River (SUR). Insects dominated the Upper River community in summer, but the Lower River community had a low proportion of insects and relatively high numbers of molluscs, ostracods, oligochaetes and hirudineans. The other summer community of the Lower River, TLR, was transitional between the winter community and the main summer one in species composition, and occurred only fleetingly in spring and autumn in the lower, more polluted parts of the zone, while persisting for most of the summer in the upstream, least polluted parts of the zone.

The trend through the study area was one of winter communities persisting longer the closer they occurred to the source of the river, and of summer communities replacing them as they disappeared, where time allowed. Multiple discriminant analyses of the faunal and water-quality data revealed a strong correlation between the distribution

of the animal communities and the quality of the water, with dissolved oxygen content, water temperature, pH and alkalinity being the factors that differed significantly between communities. The distribution of the communities also gave a clear indication of the low productivity of the Mountain Stream, for the turn-over time of the winter community there was double that of the winter community in the Lower River.

Abundance and biomass of the stony-bed invertebrates increased downstream (Part 2), with the summer community of the Lower River having the highest levels of each recorded in the study. As the trend could be correlated with the downstream increase in the nutrient content of the water, which was especially obvious in summer, the quality of the water became implicated in the high, summer-time levels of abundance and biomass in the Lower River, as well as in the spatial and temporal changes in community structure in the study area as a whole. The data clearly showed the downstream increase in secondary productivity, and the low level of secondary productivity, of the Mountain Stream.

Interpretation of the data in Part 2 was simplified by the knowledge of the times of occurrence of the different communities, for I was able to follow the appearance and decline of each community. Each community produced one peak in biomass and one peak in numbers, there being one peak of each per year in the Mountain Stream, which supported the year-long community, but two peaks of each per year in the Upper River and Lower River, because of the winter and summer communities

alternating there every year. The different kinds of communities produced peaks at different times in their tenure of the habitat, with the peaks in numbers and biomass usually, but not always, occurring together. For instance, the explosive increase in numbers and biomass of the stagnant- and polluted-water community in the Lower River in summer continued until winter rains diluted the water and washed the animals away, so the peaks in both numbers and biomass occurred near the end of this community's time in the river. On the other hand, the insect-dominated communities showed a decline in numbers with time, due to mortalities and, eventually, to the emergence of adults, so their peak numbers occurred early in the community's existence; their biomass levels, however, remained more or less the same until just before the community disappeared, due to the growth of the decreasing number of animals. These temporal trends in numbers and biomass of the insect-dominated communities were partly obscured in the case of the winter communities by the sudden appearance of large numbers of partially grown individuals in spring. It is thought that a large proportion of the winter fauna migrate vertically down into the river bed to avoid winter floods, and only return to the surface of the substratum en masse once current speeds fall in spring. A false peak in numbers thus occurs in these communities in spring, while the real peak must occur some time earlier in the community's life. Similarly, the times of the real peaks in the biomass of these winter communities cannot be pinpointed, but it became apparent that the biomass levels given for them in this thesis represent the standing crop of the unknown proportion of the animals which were sufficiently near the surface of the substratum to be within the reach of the sampler, and

not necessarily the standing crop of the benthic invertebrates as a whole.

It became obvious quite early in the investigations that a considerable amount could be learnt about the health of a river, simply by turning over a few stones from the river bed and ascertaining which species of Ephemeroptera were present. Thus the available data on the group were synthesised, to provide a basic account of their presence in the Eerste River. Species diversity of the Ephemeroptera, which was felt to be representative of the diversity of the fauna as a whole, decreased downstream. The physico-chemical quality of the water again was implicated in this change, for major decreases in diversity occurred at a town and at a sewage outfall. A high diversity index for the Ephemeroptera below a dam construction-site, however, indicated that these indices should be used with caution. The higher the value of the index the higher the quality of the water is assumed to be, yet in the silt-laden waters below the dam, where animals were rare, the index value was high because the few animals present were of several different species. In the presence of other kinds of pollutants to which the fauna could not adjust, such as toxic chemicals, similar high faunal diversity indices could result, that falsely indicated unpolluted waters.

Most of the 17 species of Ephemeroptera in the Eerste River occurred either in the dry summer and autumn or the wet winter and spring (Part 3), with the seasonality of occurrence being least obvious in

the headwaters and increasingly more obvious downstream. Many of the species had univoltine life cycles, while the rest had flexible life cycles that varied with changing environmental conditions down the river. While the univoltine species responded to downstream enrichment of the water by growing faster and larger in the lower reaches, some of the remaining species had a univoltine life cycle in the Mountain Stream, but a multivoltine one in the Lower River.

One of the major findings in Part 3 was that almost half of the 17 species are endemic to the upper reaches of streams of the south-western Cape, and are thus dependent on a rapidly diminishing habitat. As dams continue to be constructed and cause flooding of the mountain valleys of the region, these species must become more rare, and we do not know if they can re-establish themselves in the altered and regulated rivers below the impoundments. The remaining species generally occur throughout the river or in the polluted lower reaches in summer, are hardier and are more widespread over the sub-continent; thus their continued existence is not threatened to the same extent as that of the endemic species.

In each of the first three parts of the thesis there is proof of the low level of secondary production in the Mountain Stream. As these shaded, nutrient-poor headwaters appear to be heterotrophic and therefore largely dependent on litter from the riparian vegetation for energy, it seemed possible that the low productivity of the aquatic fauna in the zone was related to the quantity and/or quality of this litter. Therefore, the dynamics of the allochthonous

detritus in the Mountain Stream and the Lower River were investigated and compared, and the growth of a common riverine detritivore on diets of leaves from these two zones was ascertained (Part 4). The sclerophyllous, indigenous fynbos vegetation that occurs in the mountain catchment produces about half the allochthonous detritus (2,67 t ha^{-1} yr^{-1}) that deciduous exotics in the Lower River do (4,59 t ha^{-1} yr^{-1}). The fynbos leaves leach and decay in water as quickly as do the deciduous leaves and are as palatable to aquatic detritivores. By these means, and by fragmentation and downstream drift, most leaves disappear from the river within four months of falling in the water. Though the litter disappears equally quickly from both zones, the lower input in the Mountain Stream results in detritus always being more scarce there than in the Lower River.

Peak litter-fall from the riparian trees in the fynbos biome is in summer, but the mountain-stream invertebrate community as a whole (WMS) has an annual autumn-to-summer life cycle. As most leaves entering the Mountain Stream at the time of the peak litter-fall disappear by mid-autumn, food is scarce for the newly-appeared community through most of its life cycle, and only increases in quantity in late spring, as the animals near maturity. This is in contrast to the situation in the Lower River, where the winter community (WLR) appears at about the same time as the autumn leaf-fall of the deciduous trees, and where the variety of deciduous and evergreen trees provide a more continual input of litter into the river than occurs in the Mountain Stream.

Growth of a riverine detritivore, the ephemeropteran *Castanophlebia calida* was slow in the Mountain Stream, with the emergence after 10 - 12 months of small adults, while in the Lower River the nymphs grew faster and larger and took only 5 - 6 months to complete their development (Part 3). *C. calida* is part of the winter community in each of these zones (WMS and WLR), and its growth pattern and length of life cycle in the two zones is characteristic of the two communities as a whole. In laboratory experiments *C. calida* showed no significant difference in growth rates when kept at different temperatures that were typical of the two zones in winter (10° and 15°C), suggesting that the downstream increase in its production is not due to downstream increases in water temperature. In the experiments the nymphs also grew equally fast on fynbos or deciduous leaves, provided the food was abundant, but at low food levels nymphs provided with fynbos leaves grew more slowly than those provided with deciduous leaves. If the standing stocks of allochthonous detritus in the Mountain Stream and Lower River were equal and low, then, the nymphs in the Mountain Stream could be expected to grow more slowly than those in the Lower River. Thus, the low secondary productivity of the mountain-stream community appears to be due to the quality of the detritus, the low levels of this detritus in the river, the lack of synchronisation between leaf-fall and invertebrate life cycles which results in food being scarce during much of the animals' lives, and the consequent slow growth of the animals.

The unusual summer timing of peak litter-fall from the riparian fynbos trees allows interesting comparisons to be made between life cycles

of the fauna in the Eerste River, and of that in streams in the Northern Hemisphere which receive the more usual autumnal leaf-fall of deciduous trees. The theory that detritivorous stream fauna synchronise their life cycles to benefit from the autumn leaf-fall cannot be applied to the Eerste River, where appearance of the new, year-long community in the Mountain Stream lags about three months behind peak litter-fall despite the resultant scarcity of food. The synchronisation of life cycles of stream fauna with peak leaf-fall may be a timely coincidence in some cases, for in the Eerste River the summer leaf-fall of fynbos species has shown that some other factor - possibly avoidance of high summer temperatures - is more critical to the survival of the mountain-stream community. Additionally, the suppression of growth and high mortality rate of *C. calida*, in growth experiments where the level of detritus from deciduous exotics was high, suggests that chemical changes of the water associated with the introduction of autumn-shed deciduous leaves into the Lower River, may actually be detrimental to some species if sufficient flow does not occur at the time of leaf-fall. There are thus advantages and disadvantages associated with beginning a life cycle at the time that allochthonous detritus is at peak levels on the river bed, and the response of any one species may well be a compromise based on the conflicting effects that several different factors have on its life cycle.

The work in this thesis has relevance beyond the recording of new information on South Africa's riverine fauna. For instance, the value of biological as well as chemical monitoring of water quality

is becoming increasingly recognised - most river biologists know of rivers that have been pronounced chemically acceptable, but which are devoid of life. Once the temporal and spatial distribution of the invertebrate communities in a river has been ascertained (as in Part 1), a monitoring programme based on a twice-yearly collection of water and faunal samples would provide a long-term check on the health of the river, and would help us to identify subtle environmental changes that might otherwise go undetected.

The distribution of animal communities in the river clearly showed the response of the aquatic invertebrates to the extremes of discharge and water quality that they must face over a yearly cycle. With increasing distance from the source, the annual change from winter to summer fauna and back again became more pronouced, in a pattern that must have occurred long before man's arrival in the area. It would be interesting to know if the changes in the lower reaches were less extreme before human settlements were established (the natural poor summer flow, together with leaf-fall from riparian trees, would have resulted even then in an increase in organic material in the semi-stagnant waters), and to this end a valuable study could be made of one of the few remaining rivers in the area that run through undisturbed fynbos from source to estuary. While the fauna of the headwaters of such undisturbed rivers is undoubtedly virtually the same as that of the Eerste River, we do not know how similar the animals of their lower reaches are to those of the polluted lower reaches of rivers in developed areas.

Knowledge of the species distribution, life cycles and habitat preferences of key aquatic species, such as the Ephemeroptera, enables the ecology of different rivers to be compared. Though one or two species of Ephemeroptera present in some other local rivers are absent from the Eerste River, casual sampling in the south-western Cape has revealed few rivers in which the distribution of Ephemeroptera is fundamentally different from that in the Eerste River. The exceptions, of course, are those rivers so grossly altered by man that the Ephemeroptera can no longer exist in them and, again, a study of the lower reaches of a completely undisturbed river might produce interesting results. For the most part, however, the data given in Part 3 should allow extrapolation to other local rivers.

Studying the dynamics of allochthonous detritus in the Eerste River (Part 4) was a first step towards the aims of the future - the study of catchment areas rather than of the watery confines of the rivers, and the hoped-for eventual management of these catchments as ecological units. Much remains to be learnt, but the need for such studies of complete river systems is obvious, when one considers that virtually all South Africa's water needs are met by rivers, yet only a handfull of biologists within the country are actively involved in research on lotic systems.

Supporting Paper

HYDROLOGY AND HYDROBIOLOGY

J.M. KING, J.A. DAY, AND D.W. VAN DER ZEL

In: *Fynbos ecology: a preliminary synthesis.* South African National Scientific Programmes Report Number 40. Council for Scientific and Industrial Research, Pretoria. (1979).

HYDROLOGY AND HYDROBIOLOGY

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INTRODUCTION

Hydrology is the study of the water resources in the land areas of the world and hydrobiology the study of the associated aquatic biota. Water is a limited resource in South Africa, yet predictions indicate that the demand will treble by the year 2 000, with high-quality potable water accounting for "by far the greatest proportion" (Kriel 1976). At present, rivers supply almost all of South Africa's requirements and will probably continue to do so in the immediate future.

Rainfall in the western part of the Fynbos Biome falls almost entirely in winter but becomes increasingly non-seasonal towards the east (Figure 1). An additional orographic effect occurs in the mountains, giving increased runoff in rivers when thick clouds cover the upper catchments. Owing to the porous nature of the soils of the region, most of the rainwater in the mountain areas percolates into streams, and standing waters are confined to associated seepage areas or "sponges". On the flat coastal plains, most rainwater immediately infiltrates to lower levels, often into aquifers, and again there are few permanent lakes. Temporary ponds and wetlands, although never numerous, are more a feature of the seasonally arid areas of the west coast.

The principal lotic (running) and lentic (still) waters of the Fynbos Biome (Kruger this volume) are shown in Figure 2. With few exceptions, the rivers are short and steep and the lakes or pans (locally known as "vleis") are confined to the sandy coastal plains. These water bodies were originally situated largely or entirely in fynbos but agricultural and urban development have altered their surroundings to

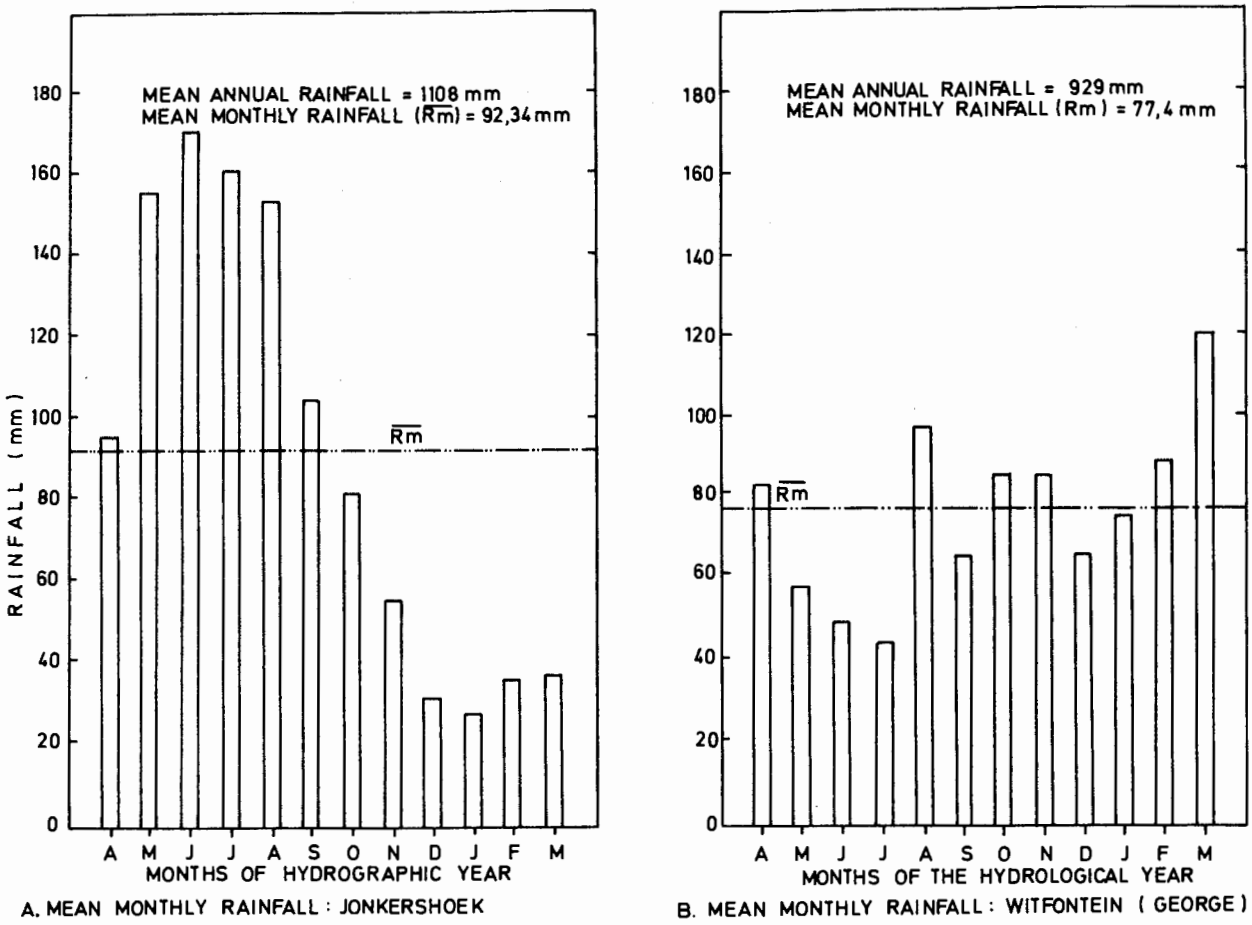

Figure 1. Average monthly precipitation for two weather stations situated in Mountain Fynbos

such an extent that the influence of fynbos on their waters can no longer be isolated except in mountain streams and a few small lakes. Here we concentrate on the untouched ecosystems while acknowledging that the others exist.

We are concerned here only with the more detailed published information. Vast amounts of raw data are stored in the records of the Department of Forestry, the Department of Water Affairs, the Department of Nature and Environmental Conservation of the Cape Provincial Administration (C P A) and the National Institute for Water Research (NIWR) of the Council for Scientific and Industrial Research.

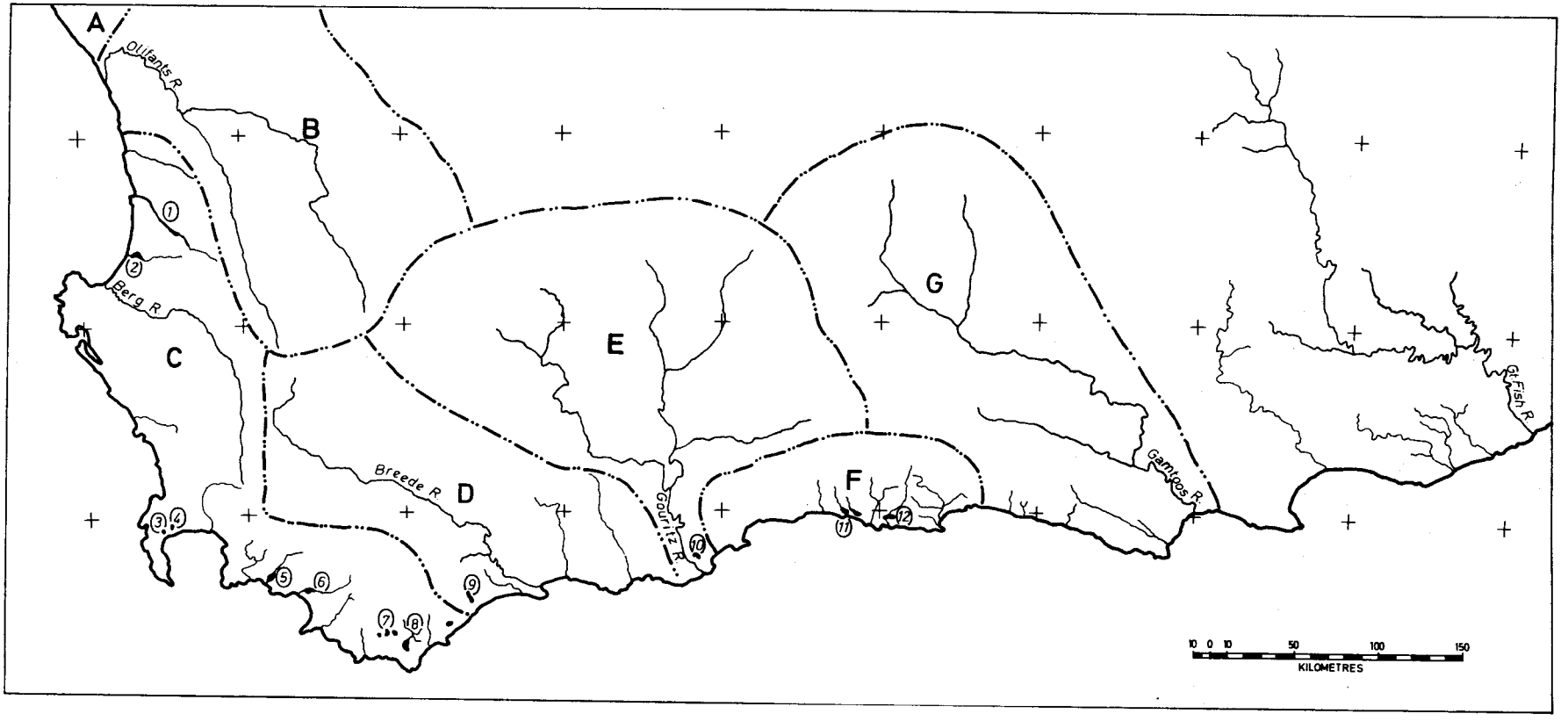

Figure 2. The principal drainage systems and standing waters within the Fynbos Biome. The contribution of the drainage systems to the South African mean annual runoff is : A - West Coast, 0,1%; B - Olifants, 2,0%; C - Berg and southwest Cape, 4,0%; D - Breede, 4,2%; E - Gouritz, 1,3%; F - Southern Cape, 1,3%; G - Gamtoos, 1,1%. The principal standing waters are : 1 - Verlorevlei; 2 - Rocherpan; 3 - Sandvlei; 4 - Seekoevlei; 5 - Bot River vlei; 6 - Klein River vlei; 7 - Bredasdorp vleis; 8 - Soetendalsvlei; 9 - De Hoopsvlei; 10 - Voëlvlei; 11 - Wilderness lakes

CHEMISTRY OF THE WATERS OF THE FYNBOS BIOME

The few reports published in scientific journals on the chemistry of the rivers of the Fynbos Biome concern the Berg River (Harrison 1958, Harrison and Elsworth 1958, Coetzer 1978a) and a number of other small rivers (Harrison and Agnew 1962). Considerably more information is available in the form of internal reports of the Cape Provincial Administration and the National Institute for Water Research. Fairly detailed data are found on the Berg River (Fourie and Steer 1971, Fourie and Görgens 1977, Fourie 1978, Hall and Görgens 1978), the Breede River (Fourie 1976, Hall and Görgens 1978) and the Eerste River (Steer 1964, Steer 1965, Steer 1966, Fourie 1978). Very little is known about lowland vleis. Published reports are available on a few small vleis in the south-western Cape (Schutte and Elsworth 1954, Harrison 1962) and on Swartvlei and Groenvlei in the southern Cape, which falls only marginally within the scope of this report. There is a single internal report on Rocher Pan in the lowlands of the west coast (Coetzer 1978b).

One feature common to all these bodies of water in their natural state is that they are oligotropic and, at higher altitudes, highly potable. This reflects low levels of nutrients in the soil (Lambrechts this volume) which are in turn reflected in the adaptations of the aquatic and terrestrial flora and fauna (King in preparation, Specht 1979, Kruger this volume, M P Hassell pers comm).

In addition to the low nutrient levels, waters of the mountain streams and high-altitude sponges have low levels of total dissolved solids (TDS), low sediment loads and are poorly buffered. Although the pH varies from river to river it seldom approaches neutrality and may be as low as 4,3. The colour is variable but often brown or "peaty", particularly on the seaward slopes of coastal mountains and to the east. In the longer rivers, TDS levels and turbidity increase in the lower reaches, resulting in a better-buffered system that is more alkaline and less brown ("white" in the literature). In low-level lakes the water tends to be white and alkaline if fed from local catchments or acid and brown if fed by mountain runoff: most of the small number of acid, brown vleis with local catchments are situated in stands of fynbos.

We have found no literature concerning the reasons for the differences in acidity and brownness of the waters of the area. The few authors discussing these factors have assumed them to be due to the presence of "humic acids" (secondary plant

compounds such as tannins and other phenolics). It is known, for example, that many nutrient-poor tropical white-sand soils produce very acidic blackwater rivers rich in these "humic acids". Janzen (1974) considers the high concentrations of secondary compounds, often found in plants growing on nutrient-deficient soils, to be used by the plants as a means of chemical defence against herbivores. It would be interesting to examine the phenomenon in the fynbos region in relation to soil nutrients, particularly since browner waters have been assumed to be more acidic, yet the headwaters of the Berg River, for example, although very acid (pH 4,3 - 5,6), are not deeply stained except during spates (Harrison 1958).

In summary, then, the brownness of water is usually, but not always, correlated with pH and is more common both on the seaward slopes of mountains and in eastern rather than western regions. In the absence of further data we speculate as follows: the brown colour is due to "humic acids". These substances are leached out of decaying vegetation, particularly in sponges and vleis, and contribute to the low pH of the water. The greater the amount of water available, the greater will be the degree of leaching from plants to water. Orographic effects on the seaward slopes of mountains and the less seasonal rainfall in the east may influence the rate of leaching from decaying vegetation and thus be at least partly responsible for the geographic variation in brownness within the Fynbos Biome. Further, rainwater percolating downwards may remain for some time as ground water, accumulating leachates; during heavy rains this water would be displaced into the stream channel causing a sudden increase in colour and decrease in pH.

In the absence of adequate chemical data it is not advisable to speculate about the reasons for the strongly acidic nature of the landward-flowing white-water streams.

LENTIC WATERS

There are few unmodified bodies of standing water left in the Fynbos Biome. Many of the larger vleis are eutrophic because of agricultural runoff and urban effluents (such as Rocher Pan - Coetzer 1978b), and owing to the seasonal nature of the rainfall in the west most of the small vleis have been enlarged or deepened to form reservoirs.

Lentic waters in South Africa have been classified by Noble (1974) and Noble and Hemens (1978). Table 1 shows the types of standing waters found in the fynbos region. The influence of fynbos is evident only in the case of restio marshes, seasonal wetlands, salt pans and acid blackwater lakelets, all of which are discussed below.

Nothing is known about reedswamps or floodplains.

Marine domination of saltmarshes is almost complete and these systems are the province of estuarine rather than freshwater biologists. A great deal of information is available on saltmarshes but will not be discussed here.

Other than the blackwater lakelets, coastal lakes are not discernably influenced by fynbos; the moderately alkaline Groenvlei has been studied by Martin (1956) and Coetzee (1978), the strongly alkaline Princessvlei and Seekoevlei by Harrison (1962) and Rocher Pan by Coetzer (1978b). There is no published information on Verlorevlei and other west coast vleis with occasional seawater input.

The estuarine lakes of the southern Cape, such as Swartvlei, have been studied by the Institute for Freshwater Studies at Rhodes University. Information is available on their origin (Hill 1975), nutrients (Howard-Williams 1977, Howard-Williams and Davies 1979), primary productivity (Robarts 1973, Robarts 1976, Howard-Williams 1978), zooplankton (Coetzee 1976) and trace metals (Watling 1979).

Fynbos-dominated wetlands and vleis

The restio marshes grade imperceptibly into the sponges at river sources. Both are important and little-known ecosystems which need attention because of their influence on water quality.

The nature of the vegetation surrounding the Cape seasonal wetlands and salt pans determines the amount and type of detritus that they receive, largely in the form of wind-borne plant matter and faeces. This in turn determines the available nutrients, while the pH and concentration of ions depend both on the vegetation and on the prevailing soil types in the region. Nothing has been published on either type of system except for a few taxonomic papers on the lower crustaceans (Sars 1896 and later, Barnard 1929).

Table 1. Types of lentic inland water systems in the Fynbos Biome (partly after Noble and Hemens 1978).

Type of ecosystem	Physical Characteristics	Characteristic flora	Characteristic fauna	Examples	Degree of influence of fynbos
Vleis and floodplains					
Restio marshes	perennially waterlogged, may accumulate peat	Restionaceae, sedges	unknown	edges of source of Berg River	strong - restios dominate
Reedswamps	permanent, very shallow	Phragmites	unknown	inlet of stream to Bot River Vlei	weak[1]
Cape seasonal wetlands and ponds	pools filling in winter from rain or stream overflow	unknown but largely microflora	lower crustaceans including phyllopods, some insect larvae	scattered on Cape Flats	moderate when nutrients derived from wind-borne fynbos detritus
Saltmarshes	saline tidal sand- and mudflats	Spartina, Zostera, Juncus, Chenopodiaceae	estuarine	Langebaan Lagoon, mouths of Olifants, Berg, Breede Rivers	virtually none
Floodplains	areas inundated by floods in lower reaches of rivers	unknown	unknown	lower reaches of Gamtoos and Olifants Rivers	unknown
Endorheic salt pans	usually dry, saline when wet	unknown but largely microflora	lower crustaceans including phyllopods	occasional small pans in region of Cape Agulhas and Bredasdorp	moderate when nutrients derived from wind-borne fynbos detritus
Coastal and estuarine lakes					
Coastal lakes with no seawater input	blackwater acid (pH 5,6 - 6,6) lakelets with no marine influence	Typha, Scirpus	insect larvae; no snails; relict marine isopods	Betty's Bay lakelets, Sirkelsvlei	strong - inflow from mountain streams or stands of undisturbed fynbos
	green or white alkaline (pH 8,3-8,9) lakes with minimal marine influence	Typha, Scirpus, Phragmites	insect larvae; no snails; relict marine isopods	Groenvlei, De Hoopvlei	weak[1]
	green or white strongly alkaline (pH 7,4 - 12,5) lakes with minimal marine influence	Typha, Phragmites, Potamogeton	insect larvae; snails; no relict marine isopods	Princessvlei, Rocher Pan, Seekoevlei	weak[1] or none - on sanddunes encroached by acacias
Coastal lakes with occasional seawater inflow	fresh to brackish with minimal marine influence	Phragmites, Myriophyllum spicatum	insects typical of still inland waters with some relict estuarine fauna	Verlorevlei and other west coast vleis	weak[1]
estuarine lakes	brackish to highly saline with dominating marine influence	Spartina and other saltmarsh flora; Potamogeton in less saline regions	largely estuarine	Sandvlei, Wilderness Lakes, Swartvlei	weak - estuarine influence dominates

1/ Quality of water largely altered by agricultural encroachment on natural vegetation.

The salt pans are few and seem to be unimportant in the overall ecology of the area, but the seasonal wetlands are visited by large numbers of birds (Cooper, Summers and Pringle 1976) and appear to be important winter feeding grounds. These seasonal wetlands are threatened in a number of ways. Many small temporary ponds are being filled in and built upon while others have been obliterated by encroaching acacias; the year-round inflow of purified sewage effluent into the Kuils River has turned several temporary vleis on the Cape Flats into permanent bogs; other vleis have been enlarged to form reservoirs on farms and often receive effluents from farm drains. We urgently need to know more about the remaining natural seasonal wetlands.

The tiny blackwater lakelets and their feeder streams in the region of Betty's Bay (Black Bass Vlei, Malkopsvlei, Grootvlei) and on the Cape Peninsula (Sirkelsvlei near Cape Point) are strongly influenced by the mountain and coastal fynbos in which they are situated. A single paper by Harrison (1962), containing all the published information which exists, is briefly paraphrased below. The lakelets at Betty's Bay were formed by the "damming effect of a low coastal range of overgrown sanddunes" and Sirkelsvlei lies in "an area of small gradients and indecisive drainage". All are small and lie on narrow coastal plains unsuitable for agriculture and are therefore almost undisturbed. The water is acid (pH 5,6 - 6,6) and strongly stained with "humic acids". Phytoplankton is minimal but the marginal vegetation is well-developed (see Table 1). Insect larvae are common, as are several species of cladoceran, ostracod and peracarid crustaceans. Snails have not been found, presumably due to the combined effect of low Ca^{++} levels and low pH on the calcification of their shells. The fauna is, however, not confined to these acid or still waters and is related to that of nearby running streams.

These lakelets offer an excellent opportunity for studying the relationships between fynbos and standing waters since they are small, of easy access and are less disturbed by human activity than most other lentic systems in the fynbos.

LOTIC WATERS

The principal drainage systems of the area are shown in Figure 2. Although their estuaries stretch over a third of South Africa's coastline, the rivers contribute only 14% of the country's total mean annual runoff, reflecting primarily the relatively low mean annual rainfall of the area (Noble and Hemens 1978).

Little published information exists on the hydrology and hydrobiology of the rivers or on the extent of pure fynbos within the catchments. It is known that several rise in high altitude sponges where the waters are acid and often darkly stained, and where peat may be present. Vegetation in the sponges consists mainly of Restionaceae and Bruniaceae with a variety of other angiosperms (Noble and Hemens 1978).

Generally the upper reaches of the rivers are steep, fast-flowing mountain streams running through Mountain Fynbos, whilst their lower reaches pass through land disturbed in a variety of ways, and where many factors affect the quality and quantity of the water. There are a few very short rivers, such as the Rooiels, which descend steeply through undisturbed fynbos to their estuaries but nothing is known about them.

The rivers are usually divided into those with clear, white, slightly acid waters such as the Olifants, Berg, Eerste and Breede and those with dark, very acid waters such as the Palmiet and Storms (Harrison and Agnew 1962, Noble and Hemens 1978). Generally the white rivers are longer with well-developed zones (mountain source, mountain stream, foothills, lower river and estuary) whilst the dark rivers change abruptly from mountain stream to estuary, reflecting their origins in coastal hills and their proximity to the sea.

In the mountain streams, marginal vegetation (that in contact with the water) is scarce and consists mainly of the palmiet (Prionium serratum) and Scirpus spp. The moss, Wardia hygrometrica, occurs on boulders, and algae typical of fast-flowing waters, such as Oedogonium sp and Stigeoclonium sp, are present but not obvious. Plankton of any kind is scarce. The aquatic invertebrates are typical of fast-flowing cold waters and whilst some may be absent from the most acid streams, none appears to be restricted to them (Harrison and Agnew 1962).

The indigenous fish fauna is dominated by cyprinids and exhibits a high degree of endemism. Seven fish species are endemic to the Olifants River system and fifteen to the fynbos area as a whole (Gaigher in prep). These fifteen species represent almost 80% of the indigenous species in the area if eels are excluded and they are generally confined to the upper parts of river systems in clear, oligotropic waters. The distribution of fish in Cape rivers has not been systematically surveyed despite the fact that the indigenous fish are increasingly threatened by introduced exotic fish and by changes in the river systems.

The scarcity of green plants as primary producers in the mountain streams has resulted in an aquatic food chain based largely on plant detritus of terrestrial origin. Detritivores are common amongst the aquatic invertebrates and these feed on decaying fynbos leaves on the riverbed. Less leaf litter falls from fynbos than from stands of deciduous trees in the lower river (King in prep) and much of that which falls into the mountain stream is carried downstream by the strong currents before it can settle on the river bed. Those leaves that do settle decay slowly because of their tough, sclerophyllous nature and because organisms causing decay are rarer in nutrient-poor than in nutrient-rich waters (Kaushik and Hynes 1971). Whether the animals feed on the leaves or on the fungi and bacteria, their food appears to be more limited in the mountain streams than in the enriched waters downstream where the banks are lined with deciduous trees. It has been shown that an ephemeropteran detritivore, Castanophlebia calida, grows more slowly and is smaller at maturity in the mountain stream/fynbos section of the Eerste River than in its lower reaches (King in prep). This tendency to low productivity in the clean mountain waters seems to be reflected in most of the aquatic invertebrates and thence through the carnivores of the ecosystem.

Most of the rivers change markedly in their physico-chemical character after leaving the mountains. Generally, nutrients, turbidity and pH increase, while flow may be poor in the lower reaches, especially in the summer in the western rivers where water is extracted for human use. The quality of the water is so altered that any residual influence of fynbos is undiscernable in these lower reaches, and they will not be considered here.

Effects of Mountain Fynbos on stream water

In high-altitude regions where mountain streams flow through stands of pure fynbos, the interrelationships between fynbos and water should be most obvious. As yet, information on the hydrological processes in these areas is sparse.

In any catchment area some precipitated water is vapourized as a result of interception and evapotranspiration by the plants and most of the remainder appears as streamflow. Catchments are in fact areas of vapour loss and the management of mountain catchments consists mainly of manipulating the vegetal cover to improve water yield (Wicht 1971). Generally forested land vapourizes

more moisture than does non-forested land, and afforestation of fynbos areas with Pinus radiata has appreciably reduced streamflow while veld burning or removing riparian fynbos has increased streamflow and reduced vapour losses (Wicht 1971).

Wicht (1974) has estimated that with an annual rainfall of 1 500 mm, protected Mountain Fynbos would evapotranspire 900 mm (60%) and produce a runoff of 600 mm (40%), and the streamflow : rainfall ratio in different areas of mountain fynbos has been given as 63 - 85% (Van der Zel and Kruger 1975) and 55% (Wicht 1971). The average streamflow : rainfall ratio for South Africa is 9%.

It seems that there is a relationship between the presence of fynbos in upper catchment areas and the presence of streams. The high-quality water in the streams is a valuable commercial commodity which is already being extensively exploited. Dams exist on several rivers and others are in the planning or construction stages, but their ecological effects on the rivers downstream have not been considered. The impoundments created are often stocked with fish although no information is available on their potential food supplies. The effects of both dams and introduced fish on the indigenous fish with limited ranges are unknown. With the demand for potable water increasing exponentially, the untouched ecosystems in the rivers' headwaters are becoming increasingly threatened.

FUTURE RESEARCH

A better understanding of the hydrological and hydrobiological processes in the fynbos area will require multidisciplinary research efforts. We feel that the establishment of a central data bank and of reference collections of both literature and of organisms are of prime importance in avoiding replication of research effort and in increasing efficiency. In this respect the synthesis and publication of the vast quantities of raw data in Departmental records and internal reports should be undertaken immediately. The lack of local taxonomists working on freshwater organisms, particularly invertebrates, is serious; encouragement of new taxonomists is essential.

Future work should be directed in two main lines :

1. Furthering the general knowledge of all water bodies in the area. This would include :

   - Studies of little-known ecosystems such as sponges, blackwater lakes, reedmarshes and floodplains and particularly those most threatened, such as seasonal waters and salt pans.

   - Investigation of the upstream and downstream effects of dams on rivers.

   - Tracing distribution patterns of aquatic organisms and identifying communities and habitats, particularly those that are threatened.

   - Investigations of the effects of urbanization, agricultural practices, encroachment of alien vegetation and recreational activities.

   - Tracing foodchains, estimating primary and secondary productivity of aquatic organisms and relating these to the chemical and nutrient status of the water.

2. Investigations of the particular relationships between Mountain Fynbos and water, particularly :

   - Tracing the occurrence and movement of rainwater on the surface, in the soil, as groundwater and in aquifers and streams, and determining how this is affected by the nature of the vegetation, the soil types and the geological formations of the catchment areas.

   - Examining the interrelations between the nutrient cycles of the soil, water and fynbos.

   - Determining the relationship between pH, colour and "humic acids" and the ways in which geological formation, soil, vegetation and aspect influence these variables.

- The quality and quantity of waters from areas of Mountain Fynbos. This is a high-priority project. Wicht (1971) states that "plants are man's most serious competitors for an adequate water ration and it has become as essential to check the vaporization drain of water to the atmosphere by manipulating vegetation as it is to reduce the flow of water to the sea by building reservoirs". Sufficient vegetation must remain on mountain slopes to prevent erosion and thus maintain the high quality of the water in the streams, but it is possible that the veld management of Mountain Fynbos will be designed to produce the maximum amount of high-quality water with little or no regard to, or knowledge of, its effect on the integrity and uniqueness of the flora. We urgently need to identify the point at which maximum water yield is accompanied by minimal damage to the fynbos.

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